

A CONTRIBUTION TO THE EARLY DEVELOPMENT OF THE HEART IN MAMMALIA, WITH SPECIAL REFERENCE TO THE GUINEA PIG

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TWENTY-THREE FIGURES

INTRODUCTION

Since the fundamental investigations on the development of the heart in mammals by His, Born, and others were published, many prominent investigators have contributed to our knowledge concerning the earlier stages of development of the heart and of the pericardial cavity in representatives of almost all classes of vertebrates. The earlier workers began their investigations after the developmental stage in which the embryonal heart tube had already assumed the complete S form. From the results of their work, however, only very general conclusions can be drawn. In many important details the literature shows contradictions, while each theory advanced has been supported by investigators of recognized ability.

The following work was undertaken at the suggestion of Professor Huber. I take this opportunity to express my hearty thanks to him for the use of his collection, which he placed at my disposal, and for his invaluable help. This work concerns itself chiefly with the origin of the endothelial tubes, the early development of the pericardial cavity, and the mode of confluence of the bilateral myocardial tubes, written with the hope of contributing something of interest to the early development of the heart.

The material for this study was obtained from many uninterrupted series of embryos of the guinea pig, from the embryological

collection in the Department of Anatomy of the University of Michigan, prepared by Professor Huber. The great majority of the embryos were fixed in Carnoy's fluid and all were cut into either cross or sagittal series at either 5μ or 7μ thickness, also a few at 10μ thickness.

In a study of the development of the endothelial and the myocardial tubes and of the pericardial cavity, to show their successive developmental changes and their relative topographical relations, a number of models were prepared according to Born's method of wax-plate reconstruction. These were made at a magnification of 300 diameters, with the aid of the projection apparatus, by superimposing the drawings of every section of the cranial part of the embryo. The thickness of the wax plates was changed in proportion to that of the sections from 1.5 to 2.1 and 3 mm., respectively. All the models described here are deposited in the Department of Anatomy at the University of Michigan.

All the figures of the sections presented here were drawn at relatively high magnifications with the aid of the camera lucida and subsequently reduced to the proper size in reproduction. The figures of the models were prepared according to the method described by Doctor Atwell. I am grateful to Doctor Guild and to Mr. Smith for help in preparing the wax plates.

LITERATURE REVIEW

Before considering the material studied in this investigation, I wish to refer to some of the theories held by earlier writers. I do not wish to give a complete résumé of the historical developments, but rather briefly to indicate the representative opinions directly concerning the subject.

In the embryonic shield of mammals at first there are present two pairs of longitudinal vessels, one of them situated near the middle line on the entoderm on each side representing the supra-intestinal longitudinal blood vessels, and the others are found primarily on the entoderm approaching the lateral margins of the embryonic shield and these representing the subintestinal longi-

tudinal blood vessels. In the cephalic portion of these latter the heart is formed, the walls of these vascular anlagen being peculiarly dilated and thickened. From this ontogenetical standpoint, the early development of the heart is merely a part of the development of the intra-embryonic vascular system.

In the survey of the literature on the subject of the origin of the intra-embryonic blood vessels in mammals, the theories held by the earlier investigators, and still maintained, can be divided into three categories.

The first theory was advanced by His, who made his observations of the flat embryonic shield of the chick. Hertwig, Kölliker, and others supported this theory. According to the *Einwachsungslehre* of His, with which the theory of the parablast was first connected, the early blood vessels of the embryonic shield are formed by a sprouting or ingrowth of the preexisting endothelial lining of the blood vessels, which had previously developed in the extra-embryonic vascular area. The ingrowth of the blood-vessel anlagen into the embryonic area takes place as solid, tenuous sprouts of the cells, which are primarily found to be anastomosed with each other, to form a close network in the area pellucida.

These sprouts of cells enter into the embryonic area through the space between the splanchnopleure and entoderm, until they reach the somitic region, where they anastomose and become canalized to form hollow vessels. Ultimately, this network of the endothelial lining forms the dorsal aortae, uniting in a longitudinal direction. The ingrowth of the endothelial sprouts is not limited to the somitic portion, but takes place also in the cranial part, entering from the lateral margin of the embryonic shield, through the space between the splanchnopleure and the entoderm, until they reach the heart anlage, where they develop the endocardium. The endothelial sprouts spread out, forming the ventral aortae and the blood vessels of the cranial region. The former blood vessels will be connected with the dorsal aortae which are prolonged cranialward by the sprouting and in the same way by turning over of the blind end of the pharynx ventralward.

Türsting studied the development of the aortae in the rabbit and confirmed the conclusion of His, namely, that these vessels are

formed by a longitudinal anastomosis of the ingrown endothelial sprouts, derived from the extra embryonic area, through the space between the splanchnopleure and the entoderm. He noticed the early connection of the dorsal aortae with the vitelline plexus.

Vialleton and Evans studied the development of the intraembryonic blood vessels in birds and came to the conclusion that in birds the greater part of the descending aortae is developed by a conversion into a continuation of the aortae of the innermost strand of the capillary plexus, extended into the embryonic shield from the neighboring yolk sac.

Lewis investigated the intraembryonic blood vessels in rabbits from eight and one-half to thirteen days after insemination, and claims that from the network of vessels in the splanchnopleure of the yolk sac all intraembryonic vessels are apparently derived as offshoots. The network ends mesially in two aortae. With the formation of the pharynx, this net is so folded as to produce dorsal and ventral aortae with the connecting first aortic arch.

Bremer recently repeated the investigation of the same material and came to practically the same results. His summary is given as follows: "In the rabbit, the dorsal aorta, the first aortic arch, the conus arteriosus, and the lateral heart are all parts of an original network of angioblast cords, derived from the extraembryonic plexus of blood vessels. Those portions of the network which are mechanically favored in their position persist, the other portions disappear. Although dealing in this paper with the development as found in rabbit embryos, I have examined various other species, as the chick, pig, sheep, etc., and feel satisfied that in all essential points the story of the development of these primary vessels in other vertebrates will be found similar to that here described."

Many other investigators support this theory, while still others do not accept it. Ranvier seems to think that the *Einwachsungslehre* of His must be regarded as a simple hypothesis, and states: "Mais il est clair qu'aucun embryologiste n'a pu suivre ce développement continu par bourgeonnement dans le corps même de l'embryon; c'est là une simple hypothèse."

The second theory of embryonic vasculogenesis was first advanced by Rabl, who asserts that the first aortic arch in amphibia

is formed by the accretion and extension of the endothelial cells proliferated in the paired heart rudiments, when these endothelial tubes were developed. Moreover, he applies this possibility to other blood vessels of the embryo, in which they are formed by the extension of the preexisting endothelial cells, as, for instance, can be seen in the regeneration of the capillaries. His statement reads as follows: "Die Beobachtung, dass bei den Amphibien die ersten Aorten Bogen durch Auswachsen des Endothelsäckchen entstehen, legt uns aber noch die Frage nach, ob es vielleicht auch das Endothel aller anderen Gefässe in letzter Instanz auf die Zellen des Endothel-säckchens zuruckzuführen sei, mit anderen Worten ob nicht vielleicht all Gefässe in' derselben oder in ähnlicher Weisse entstehen, wie die Capillaren."

Furthermore, in his later work, "The Theory of the Mesoderm," he repeated his assertion: "Ich habe die erste Entwicklung der Gefässe namentlich an den Aorten wiederholt genau verfolgt, und ist mir kein Fall erinnerlich, der mich an der Ueberzeugung irre gemacht hätte, dass neue Endothelen immer nur aus bereits bestehenden ihren Ursprung nehmen."

Rückert investigated the early development in the eggs of selachians, in which at first the subintestinal veins can be seen in the anterior embryonic shield. Here the endothelial cells are produced from the ventral angles of the lateral plates, detaching as free angioblasts, which subsequently assume forms of the cellular groups or chains between the splanchnopleure and entoderm. With regard to the anlage of the aortae in the anterior part of the embryonic shield, Rückert assumes still further that their origin is in loco and that here are anticipated the adjacent mesodermal somites, subordinately the dorsal wall of the gut comes under consideration.

P. Mayer discovered the transverse blood vessels in the eggs of the torpedo, connecting the subintestinal veins with the aortae, and he attributed their origin to the emigrated cells from the ventral parts of the mesoderm, wandering along the gut wall dorsward. Rückert agreed with the opinion of Mayer. In the vascular development of the embryo he claimed that the angioblasts still arise in loco, for example, the blood vessels of the pronephros

from the visceral walls of the somite. The angioblasts of the mandibular blood vessels from the visceral plate of the second cranial somite as well as from the wall of the foregut.

Raffaele, Emmert, and others have accepted the local formation of the embryonic blood vessels and are in agreement with the idea of Rückert. After the first publication of his work in 1888, Rückert investigated all classes of vertebrates and confirms his claims to the local formation of the embryonic blood vessels. Concerning the development of the chick, he expressed himself as follows: "So findet also beim Huhn statt des Einwachsen der Gefässanlagen eine von der Peripherie des Keimwalles gegen den Embryo zu fortschreitende Differenzierung derselben aus dem Mesoderm statt, was mit den Beobachtungen an Selachieren übereinstimmt. Auch innerhalb des Embryo entstehen beim Huhn die Gefässanlagen durch locale Ausschaltung des Zellen Materials aus dem Mesoblast, wovon ich mich bei der Herz so wie der Aortenbildung überzeugt habe."

Mollier reached the same conclusion, confirming Rückert. After thoroughly studying the material of a wide scope, he concludes as follows: "Es lässt sich also für die Genese der embryonalen Gefässe der Amnioten zur Zeit ein Urteil dahin fassen, dass die Lehre von der lokalen Entstehung der Gefässzellen auch hier Geltung besitzt und dass die von His und Vailleton gegebenen Flächenbilder, ferner die Rekonstruktionsbilder von Türling in dem Sinne zu deuten sind, dass die im Embryo sichtbaren ersten Gefässzellenstränge nicht als Sprossen ausserembryonaler Gefässanlagen entstanden sind, sondern vielmehr ihre Entstehung aus einzelnen, in loco entstandenen und netzförmig vereinigten Gefässzellen nehmen."

Sobotta not only supported the theory of Mayer and Rückert, but he also emphasized that those blood vessels found on the walls of the yolk sac were derived from the intraembryonic blood vessels as a result of their continuous outgrowth.

New light was shed on this contradictory evidence by a number of investigators who employed the methods of experimental embryology and were able to show that the yolk-sac angioblasts may be kept out of communication with the intraembryonic blood

vessels, thus lending evidence in favor of the local formation of the embryonal blood vessels.

The mechanical separation of the vessels of these two portions was employed by Gräper, Hahn, Miller and McWhorter. These workers have obtained endothelium on both sides of the chick embryo, in which one side was severed from the extraembryonic blastoderm. A further strengthening of the theory of the local formation is found in the recent experimental work by Reagan, who writes as follows: "In conclusion it is well to consider the following recently established facts which should share in defining our morphological interpretation. The yolk sac is not necessarily the site of formation of the earliest blood vessels. Intraembryonic blood vessels develop in situ when communication of the extraembryonic vessels with intraembryonic tissues is prevented by chemical or mechanical means."

The method of exposing the developing embryo to diluted anesthetics was employed by Stockard, who claimed as a result of his work that in *Fundulus* embryos the heart endothelium and the aorta arise in loco within the embryo, as the blood vessels, even the mesoderm are absent in the yolk sac in the cranial portion.

Among the investigators who have accepted the local formation of the intraembryonic blood vessels, opinions are still quite divergent at present as to from what part of the embryonal blastoderm the angioblasts are differentiated. I shall not again thoroughly discuss this point, as I have already done so in my previous paper on this subject. But I shall add that there are many authors who consider the origin of the angioblasts in mammals as derived from the entoderm. Martin figures a cross-section of a cat embryo 2 mm. long and in his prominent "*Lehrbuch der Anatomie der Haustiere*" states: Während man über die erste Entwicklung der Blutgefäße im Embryonalleib noch nicht im Klaren ist, kennt man die Bildung der peripheren Gefäße genau. Ihrer Abstammung nach sind die Innenwände (endothelium) auch der embryonalen Gefäße wie die des Herzens entodermaler Natur, während die übrige Wand vom Mesoderm geliefert wird. Ich finde bei Katze die erste gefäßbildenden Zellen und Zellgruppen ein innigsten Zusammenhand mit dem Entoderm des Darmes, ja so

gar schon rundliche Spaltbildungen in Entoderm selbst. Auch die ausserembryonalen Blutgefäße sind nach Rabl entodermalen Ursprungs." In the figure depicted by Martin, angioblasts can be seen, connected with both the mesoderm and the entoderm.

In the study of a perameles embryo of 6.08 mm. in length, Miss Parker says with regard to the origin of the endothelial cells: "The evidence of this stage does not justify any definite statement with regard to the origin of the endothelium of the heart." And, moreover, she adds, that in an earlier stage the appearance by no means excludes the possibility of the entodermal origin of the endothelium.

After investigating the origin of the endothelial and blood cells in the embryo of the ferret, Wang comes to the following conclusion: "The facts revealed by the study of the early stages in the development of the ferret point to the conclusion that, whilst blood cells and vascular endothelium are closely related to each other and are formed invariably between the mesoderm and entoderm, there is evidence to show that, in the ferret, the origins of these two vascular elements are separate and distinct—the blood cells arising from the entoderm and the vascular endothelium from the mesoderm."

"If the biphyletic origin of the blood cells and vascular endothelium is to be accepted, two more points still remain to be solved, namely, how, when, and where the first blood cells enter the circulation. Unfortunately, the ferret embryos, at present worked upon, provide no definite evidence on this point, but it is quite clear that angioblast cells are formed outside the embryonic area, and that blood vessels are formed inside the embryonic area, and are at first devoid of blood corpuscles."

We shall now briefly review the data concerning the mode of the fusion of the bilateral heart anlagen; there are many divergent opinions.

Since Hensen first declared that in mammals the heart anlage is bilateral, one on each side of the embryo not far from the mid-sagittal plane and on the ventral aspect of the pericardial cavity, it was long believed that these two lateral heart anlagen ultimately came in contact and fused together in the middle ventral

surface of the embryonic shield, forming a single secondary heart tube. Even though the secondary fusion of the bilateral endothelial tubes is universally acknowledged, there are many contradictory theories concerning the formation of the single myocardial heart anlage together with the mode of fusion of the bilateral primitive pericardial cavity. In his work on comparative embryology, Balfour thus speaks: "In mammals the two tubes out of which the heart is formed, appear at the sides of the cephalic plates, opposite the region of the mid and hind brain. They arise at a time when the lateral folds which form the ventral walls of the heart, are only just becoming visible. On the formation of the lateral folds of the splanchnic walls, the two halves of the heart become carried inwards and downwards, and eventually meet on the ventral side of the throat. For a short time they here remain distinct, but soon coalesce into a single tube."

Minot writes: "In mammals by the bending down of the layers and the expansion of the coelom the vorderdarm is shut off and the lateral heart anlagen are brought together in the median line below the vorderdarm, and there fuse into a single thick tubular wall around the double endothelial heart; it is not long, however, before the endothelial tubes also fuse into one. As in the chick the two mesothelia, when the median heart arises, form a membrane (mesocardium) by which the heart is attached to the tissue above and below; both mesocardial membranes break through, putting the two coelematic cavities into communication and leaving the tubular heart suspended by its ends."

The theory of the fusion of the lateral folds of the splanchnic walls, enclosed within the laterally placed pericardial cavities at the ventral side of the foregut in mammals, as in amphibia or birds, as many investigators have asserted and now believe, is supported by the following authorities: Balfour ('81), Strahl and Carius ('89), Tandler ('12), Wilson ('14), Bryce ('08), Minot ('92) Bailey ('12), Schultze ('15), Dandy ('10), Martin ('02), and Arey ('17). From this it would seem that, as many of the above named authors claim, the heart must be provided, at least temporarily, with a ventral and a dorsal mesocardium.

In a similar way in his valuable work on the first heart anlage, Mollier says: "Das Mesocard, ventral oder medial gelegen, ist dem dorsalen der Anamnier zu vergleichen. Ein dem ventralen entsprechendes kann erst nach dem zusammenstossen beider Pleuro-pericardialhöhlenwände gebildet werden. Beim Meer-schweinchen hingegen liegen die ersten Herzzellenstränge lateral von den Firsten der Darmfalten, und sie werden durch den Darm-schluss gar nicht unter die ventrale Darmwand verlagert, wie beim Kaninchen, sondern rücken, zwischen dorsaler und ventraler Mesocardfalte gelegen, einander näher, bis zur Berührung und endlich Verschmelzung. Doch erfolgt auch hier, wie aus der Figur ersichtlich, der Durchbruch des ventralem Herzgekröses zuerst."

Robinson has pointed out that the formation of the foregut is mainly attributed to the unproportionately rapid development of the embryo over the relatively stationary line between the embryonal and extraembryonal areas. If the idea were true, that lateral folds of the mesoderm converge ventrally until their entodermal covering has met together in the ventral middle line and both lateral pericardial cavities have fused together beneath the ventral walls of the foregut, then the heart is not only attached by the dorsal mesocardium to the foregut, but also by the ventral mesocardium to the ventral wall of the body. However, Robinson denies this generally accepted idea and the existence of the ventral mesocardium absolutely, at any time in the development of mammals, and he applies this fact to support his theory, that the separation of the foregut from the yolk sac is not due to the tenaciously held process of the tucking in of the margins of the embryonic area, but to the fact that the relatively slow-growing margin is demarcated between the embryonic and extraembryonic portions of the wall of the ovum, which rapidly increase their extent, expanding over the boundary margin. According to him, in mammals, the pericardial mesoderm is present in the pericardial portion of the embryonic area, and it is completely separated into somatic and splanchnic layers before the head fold appears. There is therefore a single pericardial cavity which extends from side to side along the anterior boundary of the embryonic shield. As the head fold is formed, the pericardial region

is reversed and it is carried into the ventral wall of the foregut, where it is present as a U-shaped tube, which communicates with the general coelom at each end. The rudiments of the heart are formed in the splanchnic layer of the pericardial mesoderm. Therefore, after the reversal of the pericardial area, they lie on the dorsal wall of the pericardial cavity, attached to the ventral wall of the foregut by the dorsal mesocardium.

Prior to Robinson, Ravn pointed out the correlation between the formation of the foregut and the forward growth of the embryonic shield. He also thoroughly described the mode of reversal in the primitive pericardial cavity.

On the other hand, many investigators believe that an active backward progression of the foregut opening occurs, in addition to the forward growth of the head fold. They deny the actual fusion of the lateral mesodermal folds in the ventral middle line. Rouviere agrees with Robinson as to the absence of the ventral mesocardium in mammals, while he does not dismiss the meaning of the forward growth of the head fold on the formation of the foregut. According to his account, in a rabbit embryo of 201 hours, both the pericardial cavities (*les deux cavités pariétales*) show the separated bilateral canal on each side, which has grown forward around the anterior end of the head fold and become fused together from a single continuous cavity in the embryo of 207 hours. The splanchnopleure forming the caudal wall of the pericardial cavity assumes a continuous fold, which Tourneux designated as the cardiac fold (*repli cardiaque*) and which he considered as growing backward automatically as a whole. As the free edge of the splanchnopleural fold has progressed always in advance of the primordial heart, no fusion of the splanchnopleure is involved and also no ventral mesocardium is formed.

In a description of the growing processes in the developing chick embryo, having kept them under direct observation while still alive, Gräper asserts that there is considerable evidence in support of the view that the margin of the foregut (*Darmforte*) moves caudally, concurrently, with the forward growth of the head fold. Moreover, he marked out diagrammatically the mode of the backward progress of the foregut opening and a quite different manner of the closure of the foregut than that of the medullary canal.

Uskow also claims the automatic backward progress of the foregut opening, according to the increase of the pericardial cavity.

In her study of the early stages in the development of marsupials, Miss Parker declares that the forward growth of the head fold doubtless plays an important part in the initiation of the formation of the foregut and that the actual backward growth of the foregut opening, but not the fusion of the lateral folds, brings about the lengthening of the foregut.

In the study of the early development of the heart and cranial blood vessels in ferret embryos, Wang agrees with Miss Parker in the absence of the ventral mesocardium, there being no fusion of this part of the pleuropericardial wall, nor that any part of the gut closure is effected by the fusion of the lateral folds.

OBSERVATIONS

Stage I

The material for this stage consists of many specimens removed from the uterus of the guinea pig thirteen days and twelve hours or fourteen days and eleven hours, respectively, after insemination. Some of them were cut longitudinally and the others transversely.

A. The first embryonic shield which came under consideration, was removed from the uterus thirteen days and twelve hours after insemination and was in a cross-section having a $7\ \mu$ thickness; 233 sections fell to the embryonic shield. The head fold had not begun to develop. The shallow neural groove was present on the surface of the embryo. The primitive streak was well developed and terminated caudally in a shallow notched groove. The mesoderm was thickened in the caudal part of the embryonic area and indicated the allantoic mesoderm. In the notochord there was present the chordal canal at its caudal end, but in other parts it was spread out to form a chordal plate through dehiscence of the ventral wall. The caudal end of the notochord was fused with an area of ectodermal proliferation at the cranial end of the primitive streak.

In the mesoderm there was observed no evidence of mesodermic somites nor could the coelomic cavity be detected. The mesoderm consisted of two lateral wings on each side in the cross-section, separated completely in the middle line by the notochord, except in the cephalad end of the embryonic shield and in the region of the primitive streak. In the cranial end of the embryonic shield, that is, the part distal to the future pharyngeal membrane, in which the ectoderm and entoderm were coalesced, the lateral wings of the mesoderm were fused, continuing caudally into the lateral wings, but sharply terminated against the extraembryonic area cranially and laterally. In this portion of the mesoderm, namely, in the pericephalic mesoderm, it formed a thinner layer than anywhere else. In the primitive streak a large mass of undifferentiated mesodermal cells was fused with both lateral wings, obliterating the demarcation between the mesoderm and ectoderm. In the mesoderm two layers of the cell band could not be distinguished; the dorsal surface of the mesoderm was, in general, compact, its outline was clear-cut; here the spindle-shaped nuclei had a relatively regular arrangement.

Between the dorsal surface of the mesoderm and ectoderm, as well as between the ventral surface of the mesoderm and entoderm, there could be distinguished clear intervals, which could be attributed in large measure to shrinkage. The mesodermal cells were spread out in two or three layers and were spindle-shaped and connected with each other by short protoplasmic processes. In the ventral surface of the mesoderm a loosening of the cell band could be seen, characterized by an increased distance between the respective nuclei. Intercellular spaces became more distinct and wider, the spindle-shaped nuclei had no definite arrangement. In nearly all sections there could be demonstrated some free, isolated cells, detached from the cell band of the mesoderm, lying between the ventral surface of the mesoderm and entoderm, as shown in figure 1. According to His, these cells are identical with the angioblasts. In some sections the angioblasts are connected with the indented ventral margin of the mesoderm by broad protoplasmic bridges;

in some other sections the protoplasmic bridges are narrow, the cells are distinctly pedunculated; in still other sections they are joined to the mesoderm by faint fibrils. Frequently a mitotic figure can be recognized in the mesodermal cells, adjacent to the angioblasts. These findings show that there can be no doubt of a distinct proliferative activity of the mesodermal cells; furthermore, every transitional feature of the migration or the detachment of the mesodermal cells, which apparently are destined to become angioblasts, point out the fact that these angioblasts have originated in the ventral surface of the mesoderm.

Figure 1 was reproduced from the forty-ninth section, counting from the cephalic border of the embryonic shield, and

LEGEND LETTERS FOR ALL THE FIGURES

<i>A.</i> , atrium	<i>F.G.O.</i> , foregut opening
<i>Am.</i> , amnion	<i>I.M.S.</i> , intermesocardial space
<i>Ang.</i> , angioblast	<i>L.P.C.</i> , lateral pericardial cavity
<i>Ao.</i> , aorta	<i>M.C.</i> , myocardial cavity
<i>A.V.C.</i> , atrioventricular constriction	<i>Mes.</i> , mesoderm
<i>A.V.Ca.</i> , atrioventricular canal	<i>M.G.</i> , medullary groove
<i>B.</i> , bulbus cordis	<i>M.T.</i> , myocardial tube
<i>B.V.C.</i> , bulboventricular constriction	<i>N.</i> , notochord
<i>C.M.L.</i> , craniomedian limb of the pericardial cavity	<i>P.</i> , pericardium
<i>Co.</i> , coelom	<i>P.C.</i> , pericardial cavity
<i>D.M.</i> , dorsal mesocardium	<i>P.M.</i> , pharyngeal membrane
<i>D.W.P.</i> , dorsal wall of pericardium	<i>P.P.P.</i> , pleuropericardial passage
<i>Ect.</i> , ectoderm	<i>S.A.C.</i> , sino-atrial constriction
<i>End.</i> , endothelium	<i>Som.</i> , somatopleure
<i>Ent.</i> , entoderm	<i>Spl.</i> , splanchnopleure
<i>E.O.</i> , endothelial offshoot	<i>S.R.</i> , septum ridge
<i>E.T.</i> , endothelial tube	<i>S.V.</i> , sinus venosus
<i>F.G.</i> , foregut	<i>T.A.</i> , truncus arteriosus
	<i>V.W.F.</i> , ventral wall of the foregut

Fig. 1 The 49th section of a series of 233 cross-sections of 7 μ thickness of an embryonic shield of the guinea pig, removed 13 days 12 hours after insemination. The early stage of the formation of the angioblasts from the ventral surface of the mesoderm. $\times 150$.

Fig. 2 The 41st section of a series of 237 cross-sections having a 7 μ thickness, removed from the uterus of a guinea pig 14 days 11 hours after insemination. The ventral surface of the mesoderm becomes loosened and angioblasts are separated. $\times 150$.

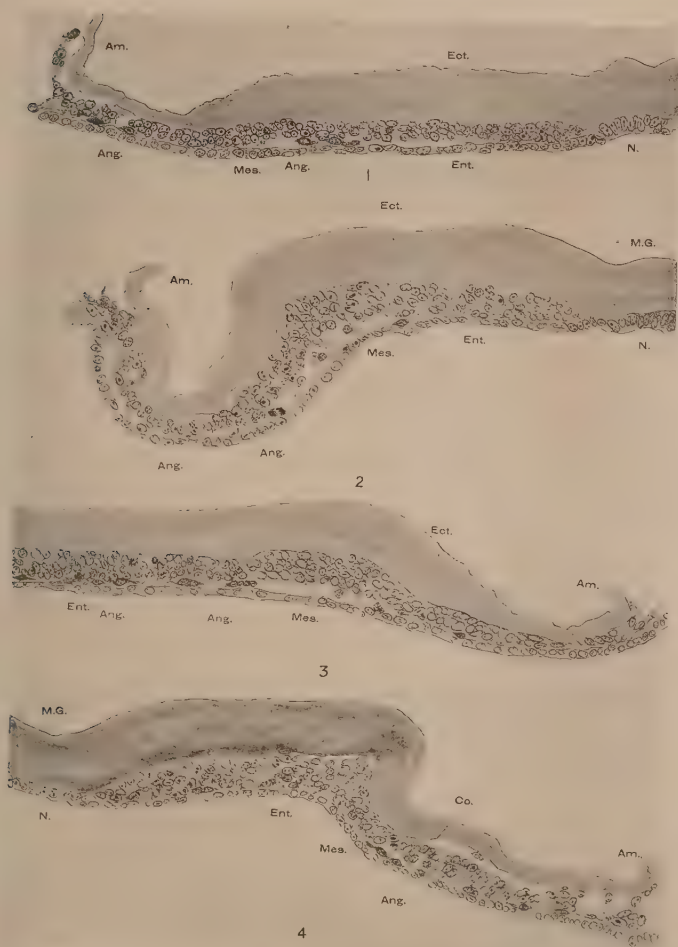


Fig. 3 The 40th section of a series of 162 sagittal sections having a 7μ thickness. This embryonic shield was removed from the uterus of a guinea pig 13 days 12 hours after insemination. The angioblasts form the cell strands between the splanchnopleura and entoderm. $\times 150$.

Fig. 4 The 63rd section of a series of 300 cross-section of 7μ thickness of an embryonic shield of a guinea pig, removed 13 days 11 hours after insemination. In the lateral plate of mesoderm the discontinuous coelom is present. $\times 150$.

corresponds approximately to the future hindbrain region, in which region endothelial tubes had been differentiated from the angioblasts in the next stage. As the contour of the entoderm is distinctly demarcated from these cells in our specimens, as the figure shows, it may be excluded from direct participation in the formation of these cells.

B. The next embryonic shield selected for discussion was removed from the uterus of a guinea-pig fourteen days and eleven hours after insemination. It is cut in cross-sections, having a $7\ \mu$ thickness, and 237 sections fall to the embryonic area. The flat incipient head fold has begun to develop, marking definitely the cranial margin of the neural plate. In this portion the ectoderm has been elevated above the surrounding embryonic shield. A broad and shallow neural groove, which gradually narrows cephalad, is present on the surface of the embryo. The primitive streak is well distinguished on the embryonic surface as of a transitional portion from the cranial neural groove into the caudal primitive groove. The notochord has acquired a tubular form at its caudal end in some more anteriorly placed portions, but in the majority of the sections its ventral wall is opened into the yolk sac, to form the chordal plate. The caudal end of the notochord is fused to the cranial part of the primitive streak. No mesodermal somites are recognized nor can any indication of the coelomic cavity be detected.

Figure 2 was reproduced from the forty-first section, counting from the cephalic amnion attachment. The mesodermal layer is thicker than that found in the preceding specimen; this is due partly to the numerical increase of its component cells and partly due to a loosening of the arrangement of the cells. In the mesoderm no layers can be distinguished, the spindle-shaped cells having no definite arrangement. The loosening of the cell is more readily demonstrable on the ventral surface of the mesoderm; its ventral outline forms a zigzag contour, due to the shorter or longer protoplasmic processes which are seen extended from the ventral row of the mesodermal cells toward the underlying space. Moreover, as can be pointed out in the figure, some cells are projected into the underlying space beyond

their surrounding group of cells, while others present a mitotic figure and have their axis directed to the space under the mesoderm and are pedunculated into the underlying space, but remain connected with the mesodermal layer by means of their narrow protoplasmic bridge. There can be seen a few spindle-shaped cells, which appear completely detached from the mesoderm and lie scattered between the mesoderm and entoderm. The area of the distribution of these cells, which we regard as angioblasts, more numerous in this embryo, extends over a wider range than is observed in the previous embryo. A glance at the figure will prove that the origin of these cells is derived from the mesoderm of the splanchnopleure.

In figure 3 there is presented a drawing of a sagittal section of an embryonic shield of approximately the same stage of development as that described under figure 2.

This series belongs to an embryonic shield of a guinea pig, removed from the uterus thirteen days and twelve hours after insemination. It includes 162 sections, having a $7\ \mu$ thickness.

The figure was reproduced from a drawing of the fortieth section, counting from the lateral amnion attachment. This section passed through the flat head fold near its lateral margin. The line of sectioning in this series was almost parallel to the mid axis of the embryonic shield. A study of the series shows that the developmental stage is just prior to the formation of the first mesodermal somite, which is indicated but not completely formed. The primitive streak extends approximately a third of the length of the embryonic shield. The general finding of the mesoderm is similar to that of the foregoing specimen. In the midsagittal plane the cranial end of the chordal plate terminates insensibly in the entoderm, where the pharyngeal membrane will be recognized. Cephalad to this membrane the pericephalic mesoderm is observed; its cranial limit terminates freely at the cranial amnion attachment. This pericephalic mesoderm is continued into both mesodermal wings caudolaterally. The ventral surface of the mesoderm is loosened and presents a coarse appearance. Between the ventral surface of the mesoderm and the continuous layer of ectoderm angio-

blasts can be seen forming cell strands, ranging one after another, approximately parallel to the long axis. In the cross-section these cell strands may be shown as single cut cells. The faintly stained protoplasmic processes or slightly rotated, tenuous protoplasmic fibrils are given off from the surface of the cell strands. Some of these anastomose with each other and others are connected with the cells of the adjacent mesoderm. In this fashion their protoplasmic fibrils form a kind of feltwork between the mesoderm and entoderm. In brief, it is only a repetition of the processes which produce the angioblasts from the mesoderm of the splanchnopleure, as observed in the preceding embryo, but the angioblasts are a step further differentiated.

C. In figure 4 there is presented a cross-section drawing of an embryonic shield of a guinea pig, removed from the uterus thirteen days and eleven hours after insemination. This series includes 300 sections, having a $7\ \mu$ thickness. In actuality this embryo presents only a slight advance in development over that discussed under figures 2 and 3.

The first mesodermic somite is indicated, but not completely formed. The intraembryonic coelomic space, which may be regarded as the future primitive pericardial cavity, considering its topographic position, shows simply a beginning of a very narrow cleavage in the lateral mesoderm of the cranial portion of the embryo. In some sections the two layers of the lateral plate of the mesoderm are separated from each other, and there can be seen narrow, discontinuous clefts between the mesodermic layers, while in other sections the whole mesoderm remains apparently solid. As a transition of these two extremes, in still other sections the coelomic space is shown as little more than a lineal cleavage. In brief, the coelomic cavity is forming from multiple foci and is not connected with the extraembryonic coelom. In the pericephalic mesoderm no coelomic space can be seen.

The figure reproduces a drawing from the sixty-third section, in which there can be seen an irregularly outlined splanchnopleure, from a relatively clear-cut contour of the somatopleure, separated by an incipient slip of the coelomic space. The

splanchnopleure shows a slightly thicker layer of spindle-shaped cells; in some of them mitotic figures are present, indicating a proliferative activity. A number of angioblasts are scattered singly, while some others are grouped in a flat strand between the ventral surface of the mesoderm and entoderm.

Practically the same stage of development as that described in figure 4 can be seen in an embryonic shield, removed from the uterus fourteen days and four hours after insemination.

In figure five we see a drawing of the thirty-second section, counting from the lateral amnion attachment. This series, cut in the sagittal plane, includes 156 sections, having a $7\ \mu$ thickness. This section passes through the well upwardly projected head fold near its uplifted lateral margin. Under this head fold there can be recognized five discontinuous coelom spaces in the lateral plate of the mesoderm, each of which is interrupted by a substantial bridge. The mesodermal cell layer of the splanchnopleure is distinctly thickened and loosened. The spindle-shaped mesodermic cells assume a somewhat irregular arrangement. A number of them have disposed themselves in such a direction that their long axis is vertical to the ventral surface. A number of angioblasts are scattered under the mesoderm of the splanchnopleure and some of them are connected with this layer by their protoplasmic processes. Mitotic figures, seen in some of the mesodermal cells, show their proliferative activity. In some of the sections the discontinuous coelomic space can be seen in the pericephalic mesoderm, but it entirely disappears as it approaches the midsagittal plane, where the mesodermic layer has remained still in a solid condition, as can be found in figure 5B. In this respect this embryonic shield differs from that shown by Robinson and of several other workers. Robinson says that in mammals the mesodermic layer extends through the pericardial portion and is cleft into somatic and splanchnic layers before the head fold is formed. In our specimens the intraembryonic coelomic space is present discontinuously in the cranial region of the embryonic shield and totally absent as it approaches the middle plane of the pericephalic mesoderm, even though the head fold is already formed.

Stage II

The material on which the following description of stage II is based consists of several embryos, certain of which are cut transversely and others longitudinally.

A. This specimen was removed from the uterus of a guinea pig fourteen days and eleven hours after insemination. The series includes 307 cross-sections, having a $7\ \mu$ thickness. A plastic reconstruction of the cranial portion was made with the Born method, and the whole shield, reconstructed for another purpose, was used for this study. This embryonic shield, as the model shows, presents a flat head fold, which is slightly more elevated than in the previous stage. The head fold can be divided into two primary parts. The cranial part is long and wide and projects over the cranial and lateral walls of the cranial body elevation. The caudal part is small and passes insensibly into the spinal portion. There is present a well-developed medullary groove in the cranial portion of the embryonic shield and its caudal end becomes gradually shallower until it disappears at the primitive streak in the caudal fourth of the embryonic shield. Its cranial end is terminated near the cranial extremity of the head fold. The deepest portion of the medullary groove corresponds to the region of the hindbrain plate. A well-marked anlage of the trigeminus is present as a thickening of the ectoderm. There are present three pairs

Fig. 5A The 32nd section of a series of 156 sagittal sections of $7\ \mu$ thickness of an embryonic shield of a guinea pig, removed 14 days 4 hours after insemination. The mesoderm is thickened and loosened, a number of discontinuous coelomic spaces is present, angioblasts are being produced from the splanchnopleura. $\times 150$.

Fig. 5B The 77th section of the same series from which figure 5 was drawn, passing through practically parallel to the midsagittal line. The pericephalic mesoderm shows a relatively thinner layer than elsewhere and lies anterior to the primitive pharyngeal membrane, as the foregut has not yet developed. In accordance therewith, the reversal of the preumbilical region of the embryonic body does not occur. $\times 150$.

Fig. 6 The 87th section of a series of 307 cross-sections of $7\ \mu$ thickness of an embryonic shield of a guinea pig, removed 14 days 11 hours after insemination. The pericardial cavity opens widely, under the thickened splanchnopleura the endothelial tube is first formed in this embryo. $\times 150$.

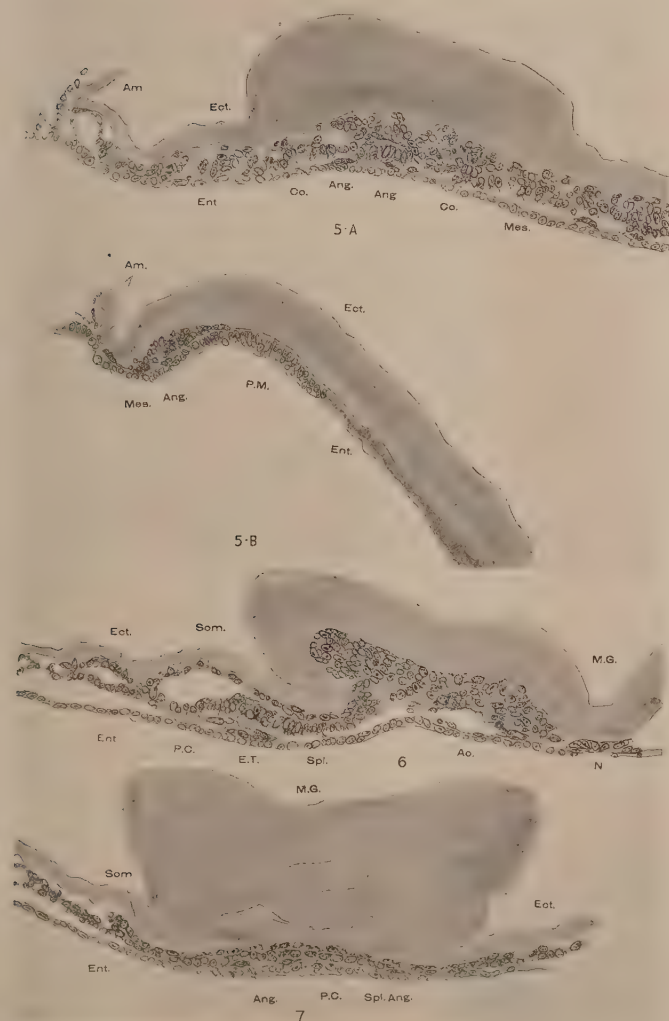


Fig. 7 The 27th section of the same series from which figure 6 was drawn, embracing the nearly anterior margin of the head fold. The pericephalic mesoderm separates into two layers, by the lineal coelem space, which continues into the lateral pericardial cavity. $\times 150$.

of mesodermic somites with a fourth pair forming. The foregut has begun to develop in the embryo; for the length of five sections its lumen is invaginated upward into the head fold.

Both the lateral primitive pericardial cavities are presented in the lateral plate of the mesoderm (fig. 6), which is completely separated into two lateral wings by the notochord, except in the cranial end of the embryonic shield, namely, beneath the cranial extremity of the head fold and in the region of the primitive streak. In these places two lateral wings come to fusion. In the mesoderm, which is produced by the fusion of both the lateral mesodermic wings in the middle line, beneath the cranial extremity of the head fold, in front of the pharyngeal membrane, a lineal cleavage can be recognized (fig. 7) by which the mesoderm is separated into two distinct layers. This coelomic space in the pericephalic mesoderm is formed by a forward extension of both the lateral primitive pericardial cavities into pericephalic mesoderm. These communicate with each other through this pericephalic coelomic space, which is now forming the craniomedian limb of the inverted U-shaped pleuropericardial cavity and may be accounted for as the essential future pericardial cavity. This cavity communicates freely with the future pleural cavity, which, in turn, passes into the peritoneal coelom. But this does not communicate with the extraembryonic coelom (fig. 8).

The reconstruction of the whole shield shows that the pleuropericardial cavity corresponds to a vague swelling presented by the ectodermal layer on the dorsal surface of the model along the lateral margins of the neural plate, and their cranial extremities are connected with each other directly beneath the cephalic end of the head fold. Therefore, the cranial extremities of the primitive pericardial cavity and of the head fold fall practically in the same level. The caudal extremities of both lateral pericardial cavities gradually disappear at the level of the caudal termination of the neural plate. And this corresponds to the gradual diminution of the prominent ectodermic swelling on the surface of the model. In this fashion, therefore, the rhomboidal shaped head fold is surrounded by

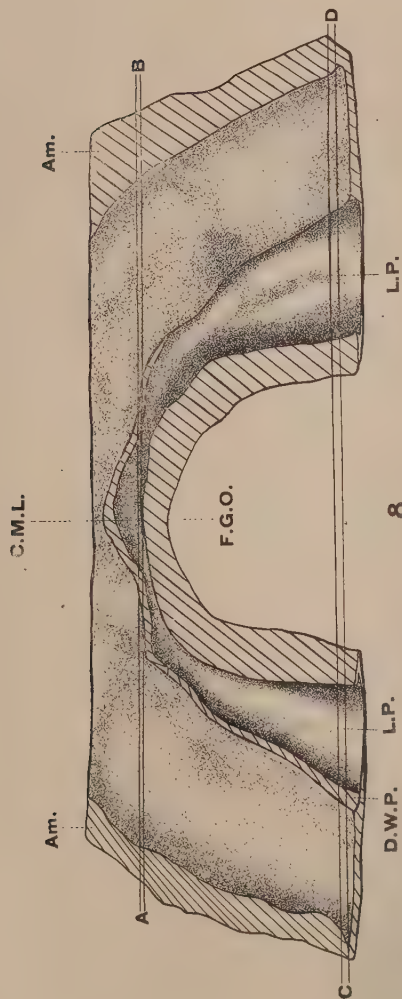


Fig. 8 Dorsal view of the reconstruction of the same embryonic shield (stage II, A), from which figures 6 and 7 were drawn. The dorsal wall of the pericardial cavity and the overhanging head fold have been removed. A-B indicates plane of section of figure 7, C-D indicates plane of section of figure 6. $\times 100$.

the horseshoe-formed primitive pericardial cavity both laterally and cephalad.

In this stage the dimension of the craniomedian limb of the pericardial cavity is yet very narrow. Its ventrodorsal extent is not more than a lineal cleavage (fig. 7), while its craniocaudal length extends throughout five sections. In tracing the lateral limbs from the craniomedian limb, however, the pericardial cavity gradually increases in width until it reaches its maximum opposite to the hindbrain region (fig. 6), and then again a gradual reduction takes place behind this region until the coelomic cavity has completely disappeared in the region of the first mesodermic somite.

On the ventral surface of the model there can be seen the crescentic gut-groove of the entoderm at the cranial portion of the embryonic shield its apex being directed cranialward and deepened gradually until it reaches the opening of the fore-gut, which is invaginated cranialward between the ectodermal head fold and the craniomedian limb of the pericardial cavity, as a horizontal diverticulum of the yolk sac. The base of the crescentic gut-groove is directed caudalward, and gradually becomes shallower, until it has entirely disappeared at the level of the hindbrain. On both sides of the gut-groove and along the fore-gut opening there is a rounded ridge running from the latero-caudal to the craniomedian end; in both position and direction, this ridge corresponds to the horseshoe-shaped pericardial cavity.

In this stage a number of angioblasts are scattered under the considerably thickened mesoderm of the splanchnopleure throughout the full extent of the pericardial cavity. A few angioblasts can be seen in the portion of the narrowly opened craniomedian limb of the pericardial space in which the mesoderm of the splanchnopleure is in close contiguity with the underlying entoderm, and they increase in number toward the lateral limbs. In some sections in which the wide open pericardial cavity is present, endothelial tubes can be seen differentiated from the angioblasts lying under the mesoderm of the splanchnopleura, which is subsequently elevated from the entoderm and projected into the pericardial cavity as a prominent fold,

as depicted in figure 6. As the differentiation of the angioblasts into the endothelial tubes takes place irregularly, the distribution of both kinds of cells intermingles irregularly with reference to the level of sections; for example, even in the wide open pericardial region in some sections a tubular endothelium appears, while in the next succeeding section there are merely scattered angioblasts or cell strands of angioblasts. For this reason the invagination of the mesoderm of the splanchnopleura into the pericardial cavity as a prominent fold cannot be attributed simply to the development of the endothelial tubes, resulting in the increase of their volume. In this embryo, generally speaking, the angioblasts apparently predominate over the endothelium.

The dorsal aortae can be seen developed in the cephalad portion of the embryonic shield, while in many sections they are present as incompletely formed endothelial tubes resting on the entoderm on both sides of the notochordal plate (fig. 6), in their caudal extent they remain as cell strands of angioblasts.

In this embryo the foregut is present as a completely formed short entodermic tube, and the gut-groove, following caudally, is shown as a deep furrow. Not until a later stage is reached are the endothelial tubes completely developed. This corresponds apparently with the development of the human embryo, as described by Graf Spee. In the slightly younger embryonic shield the coelomic cavity in the pericephalic mesoderm is not yet formed in the median plane, where this is separated in many places by thin mesodermic bridges. But this condition is only temporary and both lateral pericardial cavities will communicate with each other, as is shown in this embryonic shield.

B. In figure 9 is represented a drawing of a midsagittal section of an embryonic shield of a guinea pig, removed from the uterus fourteen days and twenty-three hours after insemination. This series includes 172 sections, having a $7\ \mu$ thickness. The figure represents a drawing of the eighty-fifth section, and this passes through the embryo just parallel and just lateral to the midaxis. As reckoned by age, this embryonic shield is just slightly older than that discussed under figures 6, 7, and 8 but,

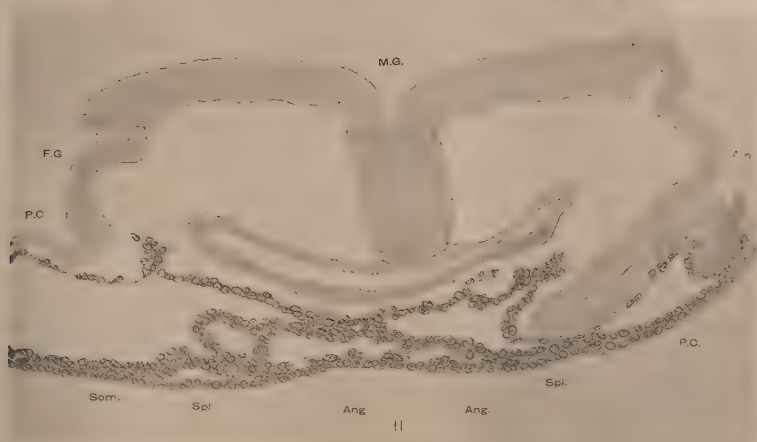
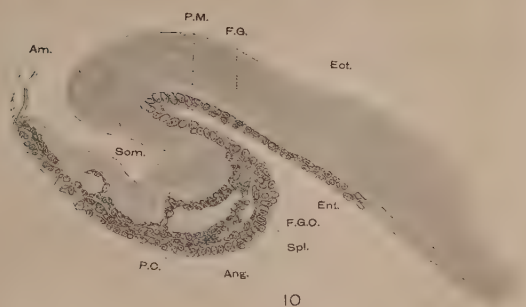
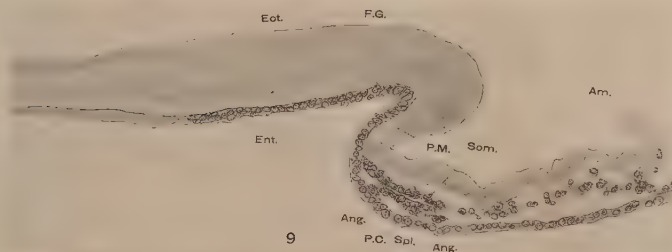
judged by the stage of general development, the same findings can be noted. Here it is noticed that the craniomedian limb of the pericardial cavity is not more than a lineal cleavage in the pericephalic mesoderm, which extends in this plane from the more anteriorly situated extraembryonic mesoderm up to the pharyngeal membrane, where the mesoderm is entirely absent and the ectoderm and entoderm are in close contiguity.

In the peripheral two-thirds of the mesoderm in this section the cells have no definite arrangement, but are loosely and irregularly scattered. This portion can be seen as a continuation of the extraembryonic mesoderm, and the same condition is shown in figure 5B in the younger stage. In the central third of its extent the two layers of the cell band can be distinguished, namely, the mesoderm of the splanchnopleura and the somatopleura, and between them lies a craniomedian limb of the pericardial cavity. Its craniocaudal extent is short and its cranial extremity is approximately on the same level with that of the head fold. Its sagittal long axis forms an obtuse angle with the sagittal long axis of the embryonic shield.

Fig. 9 The 85th section of a series of 172 sagittal sections, having a $7\ \mu$ thickness. This embryonic shield was removed from the uterus of a guinea-pig 14 days and 23 hours after insemination. The pericephalic mesoderm separates into two layers by the lineal coelem space, through which the two lateral pericardial cavities communicate with each other. The foregut has just begun to develop. $\times 150$.

Fig. 10 The 83rd section of a series of 166 sagittal sections of a $7\ \mu$ thickness of an embryonic shield of the guinea pig, removed 14 days 12 hours after insemination. The craniomedian limb of the pericardial cavity in the pericephalic mesoderm is wide open. The ventral wall of the pericardial cavity in figure 9 forms the caudal wall of it in this figure, as the reversing process occurs in the preumbilical region of the embryonic body, in conjunction with the development of the foregut, which in this embryo shows a longer lumen than in figure 9. $\times 150$.

Fig. 11 The 45th section of a series of 318 cross-sections, having a $7\ \mu$ thickness of an embryonic shield of a guinea pig, removed from the uterus 15 days 14 hours after insemination. This section passes through the forebrain plate near its anterior margin. The craniomedian limb of the pericardial cavity is wide open. The splanchnopleural fold projects into the pericardial cavity, rising from the underlying entoderm. This is especially prominent on the left side of the figure. Between the splanchnopleura and entoderm a number of angioblasts are scattered. $\times 150$.



In the younger stage the pericephalic mesoderm is situated anterior to the pharyngeal membrane, approximately in the same horizontal plane with the embryonic shield (fig. 5B). But in this stage it is brought ventrally to the pharyngeal membrane, as the foregut has begun to develop; the reversal of the pre-umbilical portion of the embryonic body accompanies this development.

C. In figure 10 is presented a drawing of a midsagittal section of an embryonic shield of a guinea pig, removed from the uterus fourteen days and twelve hours after insemination. This series includes 166 sections, having a $7\ \mu$ thickness. The figure is reproduced from a drawing of the eighty third section, passing through almost exactly parallel to the midaxis of the embryonic shield. As measured by age, this embryonic shield is slightly younger than that discussed under figure 9, but the general findings of the development are slightly in advance of that of the latter.

The craniomedian limb of the pericardial cavity, which lies under the foregut, extends dorsocaudally in a cranioventral direction, and has increased its dimensions in both the ventrodorsal and craniocaudal directions (fig. 10). Compared with the foregoing embryo (fig. 9), its sagittal long axis forms an angle a little more acute with the longitudinal axis of the embryonic body. Its caudal half presents the crescentic coelom cleavage, directing its convexity caudoventralward, while its cranial half still remains as a lineal slit. The cranial extremity of the craniomedian limb of the pericardial cavity is practically situated on the same level with that of the head fold (fig. 10). It may be demonstrated, when we compare figures 9 and 10, that the backward movement of the foregut opening from the cranial extremity of the head fold is greater than the rate of progress of the head fold forward from a certain fixed point. This actual backward progress of the foregut opening brings about the lengthening of the foregut. The foregut in this embryo is longer than in the preceding embryo. Its cranial extremity is slightly caudad to that of the craniomedian limb of the pericardial cavity. The ventral wall of the foregut

coalesces with the ectoderm, indicating the pharyngeal membrane, while its dorsal wall corresponds to the cranial end of the notochord. The entoderm, which forms the dorsocaudal wall of the craniomedian limb of the pericardial cavity, is reflected from the foregut opening to the ventral wall of the craniomedian limb of the pericardial cavity, representing the so-called cardiac fold (*repli cardiaque* Tourneux). The cranial wall of the craniomedian limb of the pericardial cavity is formed by the ectoderm, which is reflected from the pharyngeal membrane to the proamnionic region.

A few cell strands of angioblasts can be seen between the mesoderm of the splanchnopleura and the underlying ectoderm. The splanchnopleura is present, its convexity turned caudo-ventrally, in accordance with the entodermic cardiac fold. Its central part has begun to invaginate into the pericardial cavity, rising from the underlying entoderm. Between these two layers the angioblasts are scattered.

Stage III

The material on which the description of stage III is based consists of two embryos, one of which was cut transversely and the other longitudinally.

A. This specimen was removed from the uterus of a guinea-pig fifteen days and fourteen hours after insemination. This series includes 318 sections, having a $7\ \mu$ thickness. The plastic reconstruction of the cephalic portion of the embryo was made with wax plates, and the whole shield, reconstructed for another purpose, was used for this study.

The neural groove extends from the cranial end to the caudal amnion attachment. It is wide and shallow in the caudal portion, while it is narrow and deepens toward the head fold. The head fold is divided into two primary vesicles; the cranial vesicle is wide and long, projecting laterally and cranially over the cranial and lateral walls of the cranial body elevation. The caudal vesicle is small and passes insensibly into the spinal portion. The anlagen of the trigeminal ganglia, as well as the rudiment of the otic ganglia, are to be seen. Four somites

are completely segmented, besides in their cranial and caudal territory, a somite is in process of formation. The dorsal aortae and the first aortic arch are present, while the ventral aortae are not yet completely differentiated. In the region of their anlagen the angioblasts are irregularly distributed. The foregut extends throughout twenty-two sections, appearing first in the twenty-seventh section and continuing to the forty-ninth section, while the craniomedian limb of the pericardial cavity extends throughout sixteen sections, appearing in the twenty-third section and continuing to the thirty-ninth section. The cranial end of the head fold appears in the eighth section, on account of the forward progress of the head fold. This fact can be demonstrated in the dorsal surface of the whole reconstruction model, in which the prominent swelling of the dorsal surface of the pericardial cavity is much more distinct than that of the foregoing model. The cranial extremity of the pericardial cavity disappears under the head fold slightly caudad to its cranial margin.

In this embryo the mesoderm of the splanchnopleural projects into the pericardial cavity, forming prominent folds, already presented in the previous stage, but in this stage is well developed. These folds are converted on both sides into continuous myocardial tubes. Their dorsal surfaces approach the dorsal wall of the pericardial cavity, coming nearly into contact with it. These lateral myocardial tubes are best developed at the level of the hindbrain, where they are relatively dilated and contain the well-developed endothelial tubes. On tracing cranialward, both myocardial tubes gradually diminish in height and width, until they finally disappear opposite to the foregut opening on its left side, while on the right side the myocardial tube continues into the caudad portion of the craniomedian limb of the pericardial cavity, converting it into the prominent rounded ridge of the mesoderm of the splanchnopleura. In this region the thickened mesoderm of the splanchnopleura, present as a somewhat flattened fold, is elevated above the underlying entoderm. In the space between these two layers a number of angioblasts can be seen (fig. 11 and 12). In tracing still farther cranialward, the relatively thin layer of mesoderm

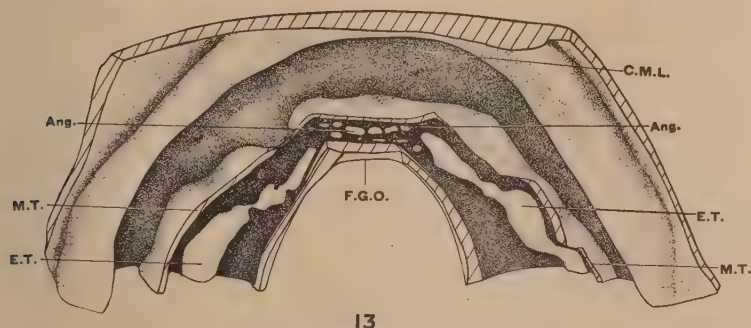
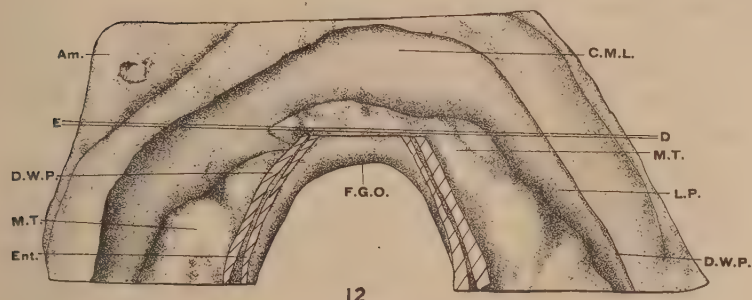


Fig. 12 Dorsal view of the reconstruction of the same embryonic shield (stage III, A) from which figure 11 was drawn. Dorsal wall of the pericardium has been removed to show the pericardial cavity and myocardial tubes. At the caudal part of the craniomedian limb of the pericardial cavity the splanchnopleura projects into the pericardial cavity, forming the prominent fold, which is absent in front of the cranial extremity of the myocardial tube on the left side. *E-D* indicates plane of section of figure 11. $\times 100$.

Fig. 13 Dorsal view of the reconstruction of the same embryonic shield (stage III, A) from which figures 11 and 12 were drawn. Dorsal wall of the pericardium and of the myocardial tubes have been removed to show the underlying endothelial tubes and angioblasts. Angioblasts are scattered under the splanchnopleural fold at the caudal part of the craniomedian limb of the pericardial cavity, almost connecting both cranial extremities of the lateral endothelial tubes. But angioblasts are absent in front of the cranial extremity of the lateral endothelial tube on the left side, where the splanchnopleura has not risen from the underlying entoderm. $\times 100$.

of the splanchnopleura remains attached to the underlying entoderm; between them no angioblasts can be seen (fig. 13).

It can be ascertained that the formation of the mesodermal splanchnopleural folds occurs in loco and progresses cranialward, until both cranial extremities of the myocardial tubes will ultimately unite and communicate with each other at the craniomedian limb of the pericardial cavity. The craniomedian limb of the pericardial cavity increases its dimensions both in the ventrodorsal and in the craniocaudal directions, while the formation of the myocardial anlage in this portion remains in its primitive condition. In the hindbrain region the pericardial cavity reaches its maximum width in proportion to the myocardial and endothelial development. But it shows here a rather narrower space in the ventrodorsal direction, on account of the dorsal expansion of the myocardial tubes. In tracing still further caudalward, the pericardial cavity gradually narrows until it entirely disappears in the somitic region, parallel with the gradually diminishing splanchnopleural folds and endothelial tubes.

The endothelial tubes are differentiated at great length, extending throughout nearly the whole extent of the lateral pericardial cavity. But in many places these tubes are irregularly interrupted, their continuity bridged by angioblast cords. The endothelial tubes terminate cranially opposite to the foregut opening on the right side and slightly caudad to it on the left side. In front of these terminations a number of angioblasts are scattered. Extending still farther craniomedially, by means of these angioblasts, the cranial extremities of the endothelial tubes are connected with each other through the middle plane underneath the flat splanchnopleural folds of the craniomedian limb of the pericardial cavity (fig. 13). There is a distinct significance in the fact that these angioblasts are directly derived from the mesoderm of the splanchnopleural cells in loco. Moreover, in some other parts the angioblasts or endothelial cells are undoubtedly connected with the thickened and indented mesoderm of the splanchnopleura. Therefore, it is conceivable that the productive activity of these cells from the mesoderm of the splanchnopleura is still continued in this embryo.

Stage IV

The material on which the following description of stage IV is based consists of two embryos, one of which was cut transversely and the other longitudinally.

A. This specimen was removed from the uterus of a guinea-pig fourteen days and eight hours after insemination. This series includes 566 sections, having a $5\ \mu$ thickness, from the cranial margin of the head fold to the caudal end of the mesodermic thickening of the allantois. The plastic reconstruction of the cephalic portion of the embryonic body was made with wax plates.

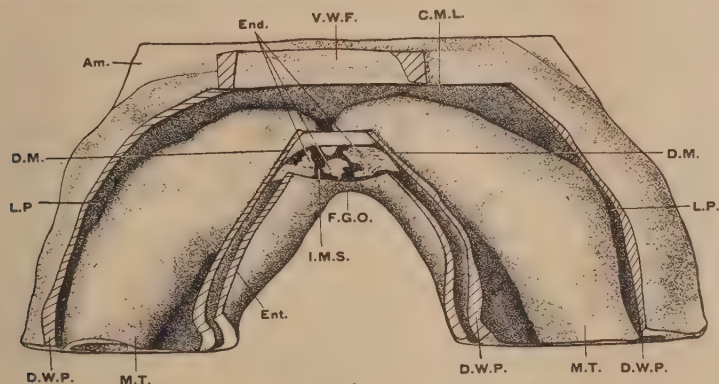
The head fold has progressed cranial- and dorsalward. Its cephalic extremity is represented in that of the embryonic shield. There are present seven pairs of mesodermic somites, the first and last being small and indistinctly segmented. The neural groove extends from the cranial end to the caudal amnion attachment. In the hindbrain region the neural groove shows very narrow and deep as both the neural plates approach each other.

In the model it can be recognized that the craniomedian limb of the pericardial cavity increases its dimensions in the ventrodorsal direction, while its lateral and craniocaudal extent remains approximately unchanged in comparison with the previous stage III. The cranial extremity of this portion extends at its dorsal part into the mesodermic cavity of the mandibular region on both sides. While their outline gradually approaches the horizontal plane, the caudal extremity of this portion is continued into both the lateral pericardial cavities, which gradually diminish in width caudalward. In the region of the second somite they entirely disappear.

The formation of both the lateral myocardial tubes, which has been discussed in stage III, are considerably developed and have so far progressed cranialward, that their cranial portions have partially come into contact and been fused together. Through this portion the myocardial tubes communicate with each other. On the dorsal surface of this fused portion of the

lateral myocardial tubes the myocardial walls are reflected directly onto the dorsal wall of the pericardium, thus forming the dorsal mesocardium on both sides. Between the lateral mesocardial layers there is present an irregular triangular space, which we purpose to designate as the intermesocardial space and through which the endothelial offshoots come out from the myocardial cavity onto the space between the mesocardial layers and the floor of the foregut. Its apex is directed cranialward, where the lateral mesocardial layers come in contact, marking the cranial margin of the communicating myocardial cavity. Its basal portion is directed caudalward and corresponds to the foregut opening, by which the lateral mesocardium layers diverge from each other and continue farther caudalward along the lateral myocardial tubes (fig. 14). Between the above-mentioned adherent cranial margin of the mesocardium and the foregut opening, the lateral myocardial cavities communicate with each other across the middle plane to the extent of eight sections. From this communicating myocardial cavity are sent out two short cranial diverticula on either side, separated by a septal wall in the middle plane, corresponding to the cranial extremities of the lateral myocardial tubes. These diverticula are present as the rounded myocardial horns, directed cranialward and separated from each other by their own inner walls. These inner walls are caudally converted into a wedge-shaped prominent ridge, which continues into the communicating portion of the myocardial cavity and gradually diminishes caudalward (fig. 15). The communicating portions of the lateral myocardial tubes are directly continued into the lateral myocardial tubes caudolaterally on both sides and they are separated from each other by the foregut opening. The ventral wall of the communicating portion of the myocardial cavity is reflected onto the ventral wall of the pericardium and is recognized only in the caudal portion. The reflection points from the myocardium to the ventral pericardial wall are fused together at the cranial part, but at the caudal part the reflection points diverge from each other and a triangular space remains between them in just the same manner as can be seen in the dorsal wall.

This ventral triangular space is covered by the entoderm cephalad to the foregut opening, while the dorsal intermesocardial space is covered by the foregut floor. Ventrally to the communicating myocardial cavity, the pericardial cavity passes from side to side, because of the absence of the ventral mesocardium. Along the ventral mesodermic reflection the anlage of the septum transversum of His will be presented in the future development, and the mesodermic reflection may be erroneously taken for



14



15

Fig. 14 Dorsal view of the reconstruction of an embryonic shield (stage IV). Dorsal wall of the pericardium has been removed to show the pericardial cavity and myocardial tubes. The two lateral myocardial tubes are partially confluent, slightly cephalad to the foregut opening. The two short cranial horns of the myocardial tubes are directed toward the top of the page. $\times 100$.

Fig. 15 Dorsal view of the reconstruction of the same embryonic shield (stage IV) from which figure 14 was drawn. Dorsal wall of the pericardium and of the myocardial tubes have been removed to expose the underlying endothelial tubes. The two lateral endothelial tubes approach most closely to each other at the confluent myocardial portion, where independent endothelial cells are interposed between the two tubes. $\times 100$.

the ventral mesocardium, if a single section of this portion should be examined, as many workers claim the existence of the ventral mesocardium in mammals.

The endothelial tubes are well developed and are enclosed within the myocardial cavities on both sides. Their lumina are patent throughout their cranial extent, their cranial extremities terminate blindly opposite to the cranial extremities of the myocardial tubes, where the myocardial tubes are projected into the pericardial cavity, like the rounded lateral horns on either side, which contain the cranial extremities of the myocardial cavity. In tracing caudally, the endothelial tubes reduce their calibers gradually and they are irregularly interrupted in their continuity by angioblasts. They entirely disappear in the somitic portion, where the lateral pericardial cavities assume a narrow and horizontal space and the splanchnopleural folds have entirely disappeared. The lateral endothelial tubes are most remarkably dilated and considerably approximated to each other at the communicating myocardial cavity, where the independent intermediate endothelial cells can be seen between the endothelial tubes. Throughout many sections in the communicating myocardial cavity, the endothelial tubes give off their endothelial offshoots from their dorsomedian aspects, coursing dorsolateralward, between the dorsal mesocardium and the floor of the foregut. These offshoots may be considered the future truncus arteriosus.

Owing to the gradual transition from these dilated endothelial tubes into the portion of the vitelline veins caudalward, their demarcation cannot be pointed out on the endothelial tubes nor on the myocardial tubes.

The dorsal aortae and the first aortic arch are completely developed, while the ventral aortae are incompletely differentiated. In their anlagen a number of angioblasts are distributed irregularly.

Stage V

The material on which the following description of stage V is based consists of two embryonic shields, which were cut trans-

versely. The partial plastic reconstruction of the cephalic portion and the reconstruction of the whole embryonic shield, made for another purpose, were used for this study.

A. This specimen was removed from the uterus of a guinea pig fourteen days and eight hours after insemination. The series includes 612 sections, having a $5\ \mu$ thickness. As measured by age, this embryonic shield is slightly younger than that discussed in stage IV. As judged by the stage of general development, it is slightly more advanced, indicated by the facts that eight somites are present and that the medullary groove is much deeper and narrower in the hindbrain region, so that to a great extent both neural plates are in contact; here it passes insensibly into the spinal region. The forebrain plate still remains wide open, projecting cranially and laterally over the cranial and lateral wall of the anterior body elevation. It is, moreover, bent considerably ventralward. In the model it can easily be recognized that, owing to the fact that this embryonic shield is considerably folded off from the yolk sac, it is in general thicker in the ventrodorsal diameter and narrower in the lateral diameter than that in stage IV. In accordance therewith, the cranial extremities of the lateral myocardial tubes are forming a more acute angle than that of the previous stage. The craniomedian limb of the pericardial cavity increases its ventrodorsal and craniocaudal dimensions, while its lateral diameter diminishes on comparison with the embryo of stage IV, in proportion to the rounded outline of this embryo. The craniomedian limb of the pericardial cavity is elongated at its dorsal part into the mandibular mesoderm. In coursing caudalward, the lateral pericardial cavities gradually diminish their width, and at the same time their outline approaches the horizontal plane as a whole. They disappear entirely opposite to the fourth somite. The direction of the lateral myocardial tubes tends to their running parallel to each other. The lateral myocardial tubes are considerably dilated at their cranial portion, where they abruptly become voluminous in comparison with their caudal portion. The transitional points of these two different portions are situated a little caudad to the foregut opening on both sides,

where the myocardial tubes mark slight indentations. These indentations indicate the future atrioventricular constriction (fig. 16).

The cranial extremities of the lateral myocardial tubes become more voluminous as compared with those of the previous stage and are projected cephalad into the pericardial cavity as large lateral rounded horns. They are separated from each other by their own inner walls, which fuse caudally into one septal wall and, as we trace still farther caudally, we find them converted into the prominent wedge-shaped ridge which projects into the communicating myocardial cavity. This ridge gradually diminishes in height caudalward until it has entirely disappeared in the middle of the communicating cavity (fig. 17).

The dorsal wall of the fused myocardial tubes is reflected directly onto the dorsal wall of the pericardium, forming the dorsal mesocardium on both sides. These lateral mesocardial layers come to fusion in a region a little cephalad to the foregut opening, where it makes the cranial margin of the communicating myocardial cavity. On the dorsal surface of the fused myocardial portion an irregular intermesocardial space can be seen, covered by the floor of the foregut. Its apex is directed cephalad, corresponding to the point where the lateral mesocardium layers are fused together. Its base is directed caudad, corresponding to the foregut opening. Its sides are formed by the lateral mesocardial layers. Corresponding to this intermesocardial space, the lateral myocardial tubes communicate with each other through the median plane throughout the extent of nine sections. In a similar way, the ventral wall of the fused myocardial tube is reflected onto the ventral wall of the pericardium, but only in its caudal portion. Between these two lines of the mesodermal reflection there remains a narrow space free from the mesoderm and covered directly by the entoderm. However, these lines of reflection on the ventral wall are disposed in a rather transverse direction and are located only for a short extent in the caudal part of the communicating myocardial tube, while on the dorsal surface the lines of reflection of the mesocardium are directed rather longitudinally and extend

throughout the whole length of the communicating myocardial tube. The communicating portion of the myocardial cavity terminates blindly in the cranial diverticulum cephalad, cor-

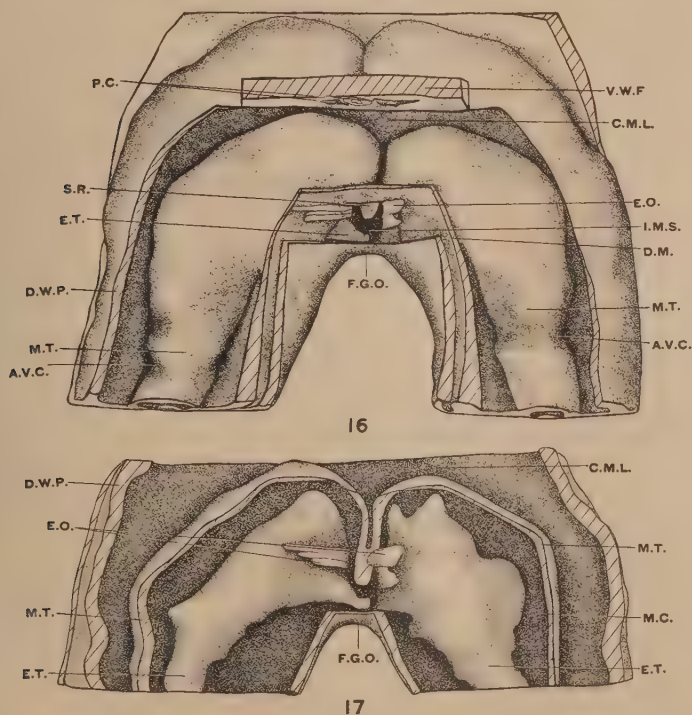


Fig. 16 Dorsal view of the reconstruction of an embryonic shield (stage V). Dorsal wall of the pericardium has been removed to show the pericardial cavity and myocardial tubes. The two lateral myocardial tubes become quite voluminous, especially at their cranial portions, which continue farther caudalward, gradually diminishing in size. The atrioventricular constriction is marked on the surface of the myocardial tubes, caudad to the foregut opening on both sides. The two cranial horns of the myocardial tubes become enlarged, and they are directed toward the top of the page. $\times 100$.

Fig. 17 Dorsal view of the reconstruction of the same embryonic shield (stage V) from which figure 16 was drawn. Dorsal wall of the pericardium and of the myocardial tubes have been removed to expose the underlying endothelial tubes, which are apparently enlarged at their cranial portions, where they most nearly approach each other. $\times 100$.

responding to the cranial extremities of the lateral myocardial tubes, while caudally it is elongated into the lateral myocardial tubes, which are diverged by the foregut opening, and their lumina are gradually diminished toward the somitic region.

In general, the endothelial tubes are much more developed than those of the previous stage, since they have become deeper and wider. At the widest portion of the endothelial tubes, corresponding to the communicating myocardial cavity, the endothelial tubes approach each other so that they come nearly into contact. On these portions, throughout many sections, the endothelial tubes give off a number of endothelial offshoots from their dorsomedian surface into the space between the dorsal mesocardium and the foregut floor. From these portions they become gradually narrower, toward both the cranial and caudal directions. The cranial extremities of the endothelial tubes terminate blindly opposite to the cranial myocardial extremities, while caudally they continue into the portion of the vitelline veins. The endothelial tubes assume the distinctly narrow calibers opposite to the atrioventricular constriction. The endothelial tubes sprout out into innumerable tenuous fibrils, often forming a feltwork, which occupies the wide space between the myocardium and the endothelium.

The dorsal aortae and the first aortic arch are developed, while the ventral aortae are not completely formed, as in their anlagen a number of angioblasts are scattered.

Stage VI

The material on which the following description of stage VI is based consists of one embryo, cut transversely. The plastic reconstruction of the cephalic portion of the embryo was made with wax plates.

This specimen was removed from the uterus of a guinea pig fourteen days and eight hours after insemination. The series includes 582 sections, having a $5\ \mu$ thickness. As measured by age, this embryonic shield is the same as that of the previous embryo. As reckoned by general development and special de-

velopment of the heart, it is considerably advanced over the preceding embryo. Eight well-segmented somites are present. The medullary groove, extending from the cranial end to the caudal amnion attachment, is as deep and narrow as in the previous embryo. The form of the embryonic shield is, in general, more rounded in comparison than with the foregoing embryo, as the ventrodorsal diameter of this embryo is apparently increased while its lateral diameter has remained unchanged. The first visceral pouch and the oral pit are developed; in these places the entoderm coalesces intimately with the ectoderm.

The reconstruction shows that at this stage of development the craniomedian limb of the pericardial cavity increases considerably in the craniocaudal dimension and in the ventrodorsal dimension. The craniomedian limb of the pericardial cavity communicates caudally with the lateral pericardial cavities. On coursing caudally, these become gradually narrower, until they disappear entirely opposite to the sixth somite. The craniomedian limb of the pericardial cavity is elongated cranially at its dorsal part into the mandibular portion, lying under the foregut floor. The caudal half of the ventral surface of the craniomedian limb of the pericardial cavity is covered by the yolk sac, while its cranial half and all other surfaces are covered by the amnion.

In this stage the fused portion of the lateral myocardial tubes increases remarkably throughout its craniocaudal extent. In accordance therewith, the cranial bilateral myocardial horns, which correspond to the cranial extremities of the lateral myocardial tubes, and predominate in the craniomedian limb of the pericardial cavity in the previous stage, apparently diminish their dimensions in this embryo, and show only their rudiments. They assume only short and wide bilateral processes, divided by a shallow and wide intervening groove. In the previous stage this groove was present as a narrow and deep sulcus. Subsequently, the inner walls of these horns diverged markedly from each other (fig. 18). The wedge-shaped ridge which, in the previous stage, projected into the communicating myocardial cavity at its middle cranial wall, as a caudal continuation

of the converted septum walls of the cranial bilateral myocardial horns, is considerably retired cranialward in this embryo. Therefore, the cranial wall of the communicating myocardial cavity approaches in such a manner toward the cranial wall of the pericardium as to come nearly into contact with it and, simultaneously, the communicating myocardial cavity is elongated cranialward. The fused portion of the myocardial tube

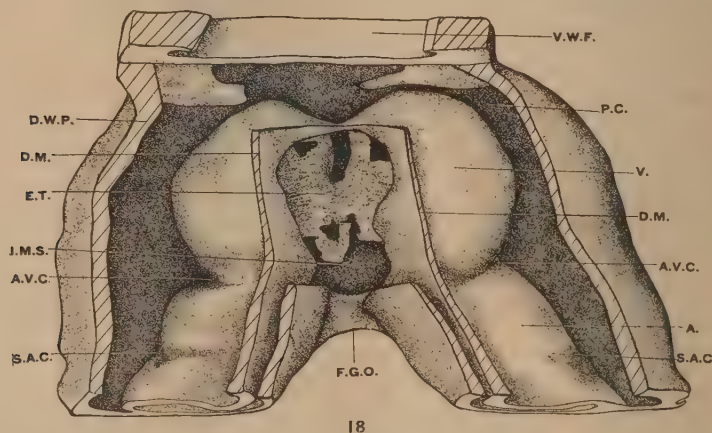


Fig. 18 Dorsal view of the reconstruction of an embryonic shield (stage VI). Dorsal wall of the pericardium has been removed to show the pericardial cavity and myocardial tubes. The confluent portion of the two lateral myocardial tubes is considerably elongated in the craniocaudal direction. The two cranial horns of the myocardial tubes diminish to short rudiments, as their septal wall retires cranialward. They are directed toward the top of the page. $\times 100$.

becomes distinctly narrower and thicker in comparison with that of the previous stage. In two of the same magnified models ($\times 300$) the widest lateral diameter of this portion is calculated as 14.5 cm. in this embryo, instead of 19 cm. of the previous embryo, while the ventrodorsal diameter of this portion presents 5.1 cm. in this embryo and 3 cm. in the former embryo.

The fused myocardial tube is reflected directly onto the dorsal wall of the pericardium, and thus forms the dorsal mesocardium on both sides. Between the lateral mesocardial layers there can be seen a long rectangular intermesocardial space; its

plane is approximately parallel with the horizontal. Its cranial margin is formed by the fused portion of the mesocardial layers in the middle line; its caudal margin corresponds to the foregut opening, while both lateral margins are represented by the lateral mesocardial layers, which continue farther caudalward, diverted by the foregut opening. In accordance with this mesocardial space, both myocardial tubes communicate freely with each other through the median plane, and thus form

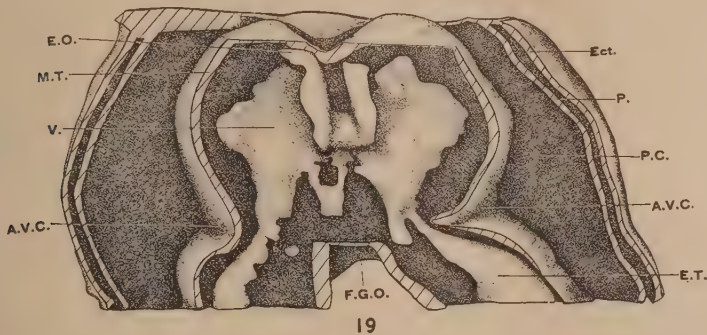


Fig. 19 Dorsal view of the reconstruction of the same embryonic shield (stage VI) from which figure 18 was drawn. Dorsal wall of the pericardium and of the myocardial tubes have been removed to expose the endothelial tubes. The two lateral endothelial tubes have fused and communicate with each other at a middle third of the ventricle, where they most closely approach each other in figure 17. The lateral endothelial tubes apparently diminish their size opposite to the atrioventricular constriction. $\times 100$.

the craniomedian limb of the myocardial cavity. This limb of the myocardial cavity is bifurcated caudally into the lateral myocardial tubes, which are diverged from each other by the foregut opening and in which the vitelline veins are enclosed, leading cranially into the craniomedian limb of the myocardial cavity (fig. 19). In brief, the myocardial anlage presents cranially two short rudimentary horns, which terminate blindly as the cranial myocardial extremities, while caudally there are two lateral myocardial prolongations, into which the vitelline veins enter. Between these four extremities the myocardial wall is relatively considerably expanded dorsal, lateral, ventralward and

contains the widest portions of the endothelial tubes, which are united in the communicating cavity. This region corresponds to the future ventricle region. On the midsagittal line of the ventral surface of this fused myocardial portion a shallow longitudinal groove can be seen.

On the ventral aspect of the fused myocardial portion the ventral myocardial layer is reflected onto the ventral wall of the pericardium, but this is limited to a short length, extending only to the caudal part of this portion.

The transition from the cranial expanding ventricle to the caudal myocardial prolongations is indicated by an annular constriction, which is produced by the infolding of the whole myocardial wall, a little deeper on the right side than on the left. This indicates the atrioventricular constriction and is situated at the level slightly cephalad to the foregut opening on both sides.

Proceeding caudally from this constriction, the lateral myocardial tubes reduce their calibers abruptly and diverge from each other. On the surface of these caudal prolongations of the myocardial tubes there are present indefinite, shallow indentations at the level slightly caudad to the foregut opening, and these constrictions have been regarded as the future sinoatrial construction.

The lateral endothelial tubes are partially fused and their lumina communicate with each other, for their inner walls have been absorbed throughout seven sections. This portion is situated in the middle third of the bulging ventricle anlage, where in the previous stage both endothelial tubes were closely approximated and presented the greatest dilation and where in this embryo also the endothelial tube is greatly expanded.

From this fused portion of the endothelial tube the two cranial horns and two caudal prolongations are given off. The bilateral cranial horns are short and gradually diminish in size cranialward, until they terminate in a pointed apex, opposite to the cranial extremities of the myocardial horns. From the dorsomedian part of these cranial endothelial horns a number of endothelial branches are given off. These endothelial

branches are connected with the ventral aortae through the intermesocardial space.

Bilateral caudal prolongations are given off on both sides from the caudal aspect of the fused endothelial tube. Continuing caudalward, both endothelial tubes gradually diminish their calibers, until the lumina have entirely disappeared at the atrioventricular constriction. Still further caudalward from this constriction, again they begin to dilate their calibers gradually and continue into the endothelial vitelline veins without any indication at their transitional point. At the atrioventricular constriction the endothelial tubes closely approach the infolding of the myocardial wall, while in the ventricle the intervening space between the myocardium and endothelium is relatively wide.

From the caudal aspect of the fused endothelial tube another intermediate endothelial branch is given off caudally. This branch is situated between the endothelial prolongations and terminates at the atrioventricular constriction.

The dorsal aortae and the first aortic arch are developed, while, in many sections, the ventral aortae are interrupted by angioblasts.

Stage VII

The material on which the following description of stage VII is based consists of one embryonic shield, which is cut transversely. The plastic reconstruction of the cephalic portion of the embryo was made from wax plates.

The specimen was removed from the uterus of a guinea-pig fourteen days and eleven hours after insemination. The series includes 418 sections, having a $7\ \mu$ thickness, from the cephalic end of the head fold to the end of the mesodermic thickening of the allantois. Nine pairs of well-segmented somites were found, each somite showing a thick wall and enclosing a uniform cavity with a compact arrangement of cells, except two caudal somites, which contained no cavity nor presented the regular arrangement of the cells.

The medullary canal is closed from the second somite to the last, but elsewhere the medullary plates remain open. The notochordal plate is separated from the entoderm throughout from the second somite to the last, but elsewhere it is still connected with the entoderm. The first and second visceral pouches are developed, in which the ectoderm and entoderm have tightly coalesced. The oral pit is formed and the pharyngeal membrane becomes quite thin.

In this embryo the pericardial cavity is closed in all directions, forming a sac, except at the dorsal part of its caudal extremities, where the pleuropericardial passages are opened on each side. These passages are represented by the narrow coelomic space, which continues farther caudalward into the peritoneal cavity and they are situated dorsomedian to the myocardial coat of the vitelline veins. From the dorsal part of the cranial extremity of the pericardial cavity a slit-like space is elongated into the mandibular region.

The surface of the pericardium is covered by the yolk sac ventrally, while laterally, cranially, and dorsally it is covered by the amnion. The pericardial cavity shows a wide space around the myocardium. Between the cranial extremity of the myocardium and the cranial wall of the pericardium there remains a wider interval than that of the embryo of stage VI.

The myocardium presents cranially an undivided cranial extremity, which expands considerably in all directions and assumes a sac form, while caudally this myocardial sac is bifurcated into two rather slender myocardial prolongations, in which the endothelial vitelline veins are enclosed on both sides. The transition from the cranial myocardial sac to the bilateral myocardial tubes is indicated by the deep atrioventricular construction, at the level slightly cephalad to the foregut opening. This constriction is produced by the infolding of the whole myocardial wall and shows apparently deeper on the right side than on the left. On the ventral surface of the ventricle there can be seen a shallow groove in the midsagittal line at its caudal half, and in accordance therewith the whole thickness of the myocardial wall is slightly infolded into the myocardial cavity.

This superficial groove and the infolding of the myocardial wall are located in the caudal half of the ventricle, for they gradually disappear toward its cranial extremity, which is of conical form. The ventral myocardial layer is reflected onto the ventral wall of the pericardium, but is confined to the atrial region to a short length opposite to the foregut opening.

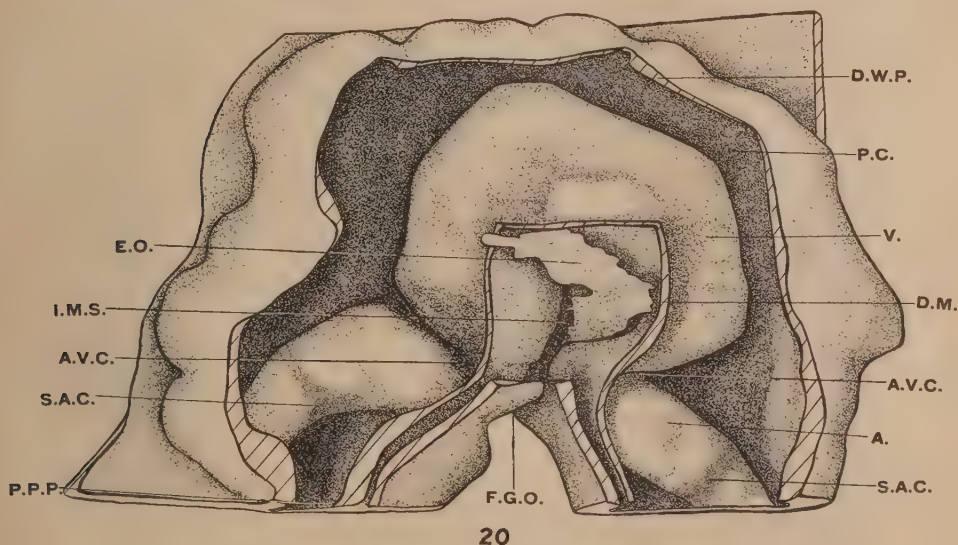


Fig. 20 Dorsal view of the reconstruction of an embryonic shield (stage VII). Dorsal wall of the pericardium has been removed to show the pericardial cavity and the myocardial tubes. The myocardium shows cranially a single sac-formed ventricle, which bifurcates into two slender myocardial tubes caudalward. The transition between them is marked by the atrioventricular constriction cephalad to the foregut opening. A single cranial extremity of the ventricle is directed toward the top of the page. $\times 100$.

On the dorsal aspect the myocardial wall is reflected onto the dorsal wall of the pericardium and forms the dorsal mesocardium on both sides. The cranial extremity of the dorsal mesocardial attachment corresponds to a middle third of the ventricle, and from this point it continues farther caudalward. Consequently, the cranial half of the ventricle is free from the mesocardium (fig. 20). Between the lateral mesocardial layers

there can be seen an irregular triangular intermesocardial space. Its plane is directed caudodorsalward on account of the abrupt dorsal expansion of the ventricle. Its apex is, therefore, situated caudoventrally and is formed by the lateral mesocardial layers, approaching contact, opposite to the atrioventricular constriction, while its basal portion is directed craniodorsally and corresponds to the portion where the lateral mesocardial layers come to fusion and mark their cranial extremities.

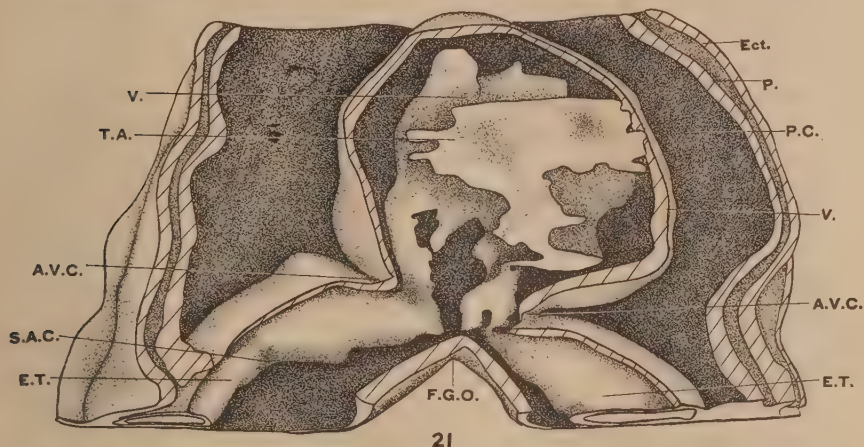
On the caudal surface of the ventricle the right half assumes an apparently wider dimension than the left. This is attributed partly to the exceeding expansion of the myocardial wall in the laterocaudal direction on the right half and partly to the deeper infolding of the atrioventricular constriction on the right side. On this bulging portion of the caudal extremity of the ventricle at the right half the caudal extremity of the right ventricle will be developed, and this is shown distinctly in the next stage.

The lateral myocardial tubes of the atrium are diverged from each other by the foregut opening. The right atrium is practically beginning just opposite to the foregut opening, while the left one begins slightly cephalad to it, for in comparison with the right side, the left atrioventricular constriction is shallower and situated slightly cephalad.

On the myocardial tubes of the atrial portion indefinite indentations, indicated as the sino-atrial constriction, can be recognized. These are between the atrioventricular constriction and the level of the pleuropericardial passages. This is especially noticeable on the left side.

The lateral endothelial tubes are fused together throughout the cranial two-thirds of the ventricle. Its cranial extremity terminates as a single conical apex opposite to the cranial extremity of the myocardial ventricle. At this fused portion the endothelial cavities communicate with each other and show considerable dilation. In tracing caudalward from this united portion, the tubes are separated from each other, even though they appear to approach each other. At the atrioventricular constriction the endothelial tubes present their smallest size and

simultaneously they approach closely to each other. Proceeding still farther caudally from this portion, they are diverged from each other by the foregut opening and again assume a gradual enlargement of their calibers. At the caudal part of the ventricle, where the endothelial tubes are separated, they present an asymmetrical size, for the right one is extraordinarily de-



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Fig. 21 Dorsal view of the reconstruction of the same embryonic shield (stage VII) from which figure 20 was drawn. Dorsal walls of the pericardium and of the myocardium have been removed to expose the endothelial tubes. The two lateral endothelial tubes have fused and communicate with each other throughout the cranial two-thirds of the ventricle. The ventricular endothelial tubes show a distinct asymmetry, due to the extraordinary enlargement of the right side, regardless of the fused or non-fused portion. The endothelial tube is elongated dorsalward from the dorsal surface of the enlarged right endothelial tube, passing through the intermesocardial space. This endothelial elongation is bifurcated into the two lateral branches, which are continuous into the ventral aortae. $\times 100$.

veloped and expended in the lateral and caudal directions, forming a curvature whose convexity is turned laterocaudalward. At this endothelial portion the endothelial tube is elongated vertically dorsalward and comes out from the myocardial cavity onto the foregut floor through the intermesocardial space. The cranial part of this endothelial elongation is bifurcated into two later branches which connect it cranially with the corresponding

ventral aortae. The asymmetrical development of the endothelial ventricle corresponds to the myocardial asymmetry in the ventricle, which has been mentioned above. In this part of the ventricle the most important change will be noted in the next stage, here developing, namely, the right limb of the ventricle. And this change is initiated in this embryo as a considerable asymmetrical expansion of the caudal extremity of the ventricle on the right side.

At the ventricle the endothelial tubes are separated from the myocardial wall by a wide intervening space, but they gradually approach each other in the direction of the atrio-ventricular constriction caudalward, as in the caudal part of the atrium no more intervening space can be pointed out between the myocardial wall and the endothelium (fig. 21).

The transition from the atrial endothelial tubes into the sinus portions can be pointed out by the abrupt decrease of the endothelial caliber on the left side, corresponding to the relatively distinct sino-atrial constriction of the myocardium. But on the right side the atrial endothelial tube continues farther caudalward without any demarcation, in accordance with the relatively indistinct myocardial constriction.

On both sides the ductus cuvieri can be seen opening into the sinus venosus. The dorsal aortae and first aortic arch are well developed, while in many places the ventral aortae still retain the plexus form.

Stage VIII

The material on which the following description of stage VIII is based consists of one embryonic shield, which is cut transversely. The plastic reconstruction of the cephalic portion of the embryo was made; the reconstruction of the whole embryonic shield, made for another purpose, was used for this study.

This embryo was removed from the uterus of a guinea pig fourteen days and twelve hours after insemination. The series includes 408 sections, having a $10\ \mu$ thickness, from the cephalic end of the head fold to near the caudal extremity of the allantoic mesodermic thickening. Nine pairs of the well-seg-

mented somites are present and the tenth is in process of formation; each somite shows the thick wall and encloses a uniform cavity. The neural canal is closed from the region of the hindbrain to the region of the last somite, though in the fore- and midbrain region it still remains open. The cranial flexure is shown in the region of the midbrain and that of the forebrain is bent downward and forward, bringing it to a plane parallel with the long axis of the hindbrain. The foregut is closed to the first somitic region. The first visceral pouch is found in the region of the midbrain with the entoderm and ectoderm coalesced, while the second visceral pouch is in process of formation also in the region of the hindbrain, in which region between the entoderm and ectoderm a thinner layer of the mesoderm than elsewhere is found interposes. The oral pit is well formed, the pharyngeal membrane is present as a thin single layer of cells. On the ventral surface of the model the edge of the foregut opening is elevated by two prominent limbs, which on each side are confluent into an extensive ventral bulging cranially to the foregut opening. In position and direction this corresponds to the pericardial cavity, containing the voluminous heart.

The pericardial sac is closed except at the dorsomedian part of its caudal extremity, where the pleuropericardial passages are found. In the region of the sinus venosus each one of the bilateral pericardial cavities is divided into a median and a lateral part by the myocardial fold and in the region of the pleuropericardial passages the lateral parts of the bilateral pericardial cavities terminate blindly caudalward, so that only their median portions are continued caudally into the peritoneal cavity. Accordingly, these passages are represented merely by narrow, crescentic coelomic spaces, dorsomedian to the vitelline veins, proceeding caudally and mesially, crossing with the vitelline veins, which run cranially and mesially.

On account of the considerable enlargement of the muscular heart, the pericardial space is, in general, proportionately reduced, especially in the well-developed ventricular portion a simple narrow space surrounds the muscular sac of the ventricle.

In the region of the atria and the sinus venosus a relatively wide space intervenes between the rather flat muscular tubes and the pericardial wall (fig. 22). There are present two distinct constrictions on the tubular muscular heart, infolding the whole thickness of the myocardial wall, one of which represents the atrioventricular constriction and the other the sino-atrial constriction.

The atrioventricular constriction is present asymmetrically on both sides; on the right side it is marked more deeply and situated slightly caudad, while on the left side it is shallower and lies a little cephalad. Therefore, this constriction forms an oblique angle with the long axis of the muscular heart.

On the contrary, the sino-atrial constriction is marked more deeply on the left side and is situated slightly cephalad to the foregut opening, while on the right side it is less deeply constricted and is situated slightly caudad, just opposite to the foregut opening.

The ventricle can be divided into two lateral limbs by a ventral and a dorsal longitudinal sulcus. On the dorsal surface it is marked along the attachment line of the dorsal mesocardium and terminates caudally opposite to the right margin of the atrioventricular constriction, while its cranial extremity gradually disappears at the portion where the bulbus cordis is differentiated from the dorsal wall of the ventricle. On the ventral surface the longitudinal sulcus extends to a caudal third of the ventricle.

At the caudal part of the ventricle, for a short length, both lateral limbs are divided into two completely independent cavities by the septal wall. The caudal extremity of the right ventricle is shown as the conical process, projecting caudo-laterally and terminating blindly, while at the caudal extremity of the left ventricle the atrioventricular canal opens, which is formed by the infolding of the muscular wall, corresponding to the atrioventricular constriction.

The septal wall between the two lateral limbs at the caudal part of the ventricle is farther continued cranialward and is converted into wedge-shaped prominent ridges at the inner sur-

face of the ventral and dorsal wall of the ventricle, in relation with longitudinal sulci on the external surface. These ridges have gradually disappeared within a caudal third of the ventricle (fig. 23). These prominent ridges show their anlage only

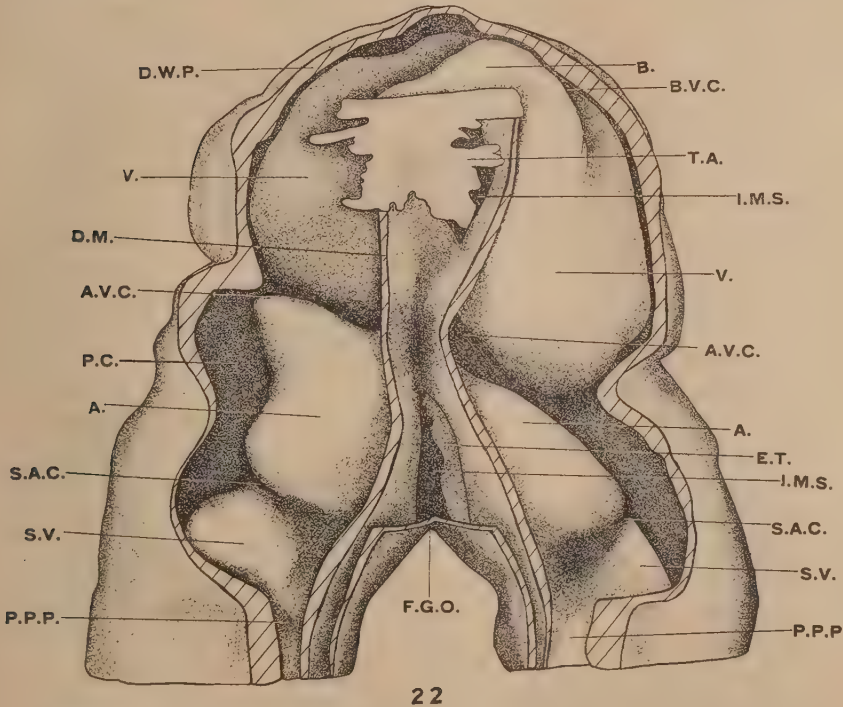


Fig. 22 Dorsal view of the reconstruction of an embryonic shield (stage VIII). Dorsal wall of the pericardium has been removed to show the pericardial cavity and myocardium, which is subdivided into several individual portions (bulbus cordis, ventricle, atrium, sinus venosus, etc.) by the distinct bulbo-ventricular atrioventricular, sino-atrial constrictions. $\times 100$.

on the ventral wall of the ventricle, near its caudal end, as seen in the previous stage. Consequently, there can be but little doubt that these folds cannot be regarded as the remnants of the primitive cardiac septum.

The bulbus cordis is differentiated from the dorsal wall of the right ventricle near its cranial end, bulging out its wall cranial-dorsal and laterally. Its ventral wall is distinctly separated from the dorsal wall of the right ventricle at its cranial portion, projecting cranialward as an independent muscular sac, while in its caudal portion there can be noted no distinct demarcation between the wall of the bulbus cordis and that of the right ventricle. At the left and cranial sides of the bulbo-ventricular junction, a deep external furrow can be seen, accompanied by a consequent infolding of the muscular wall. On the right side the bulboventricular furrow is indefinitely marked only its cranial part, while in its caudal part it has disappeared entirely and insensibly continues into the dorsal wall of the right ventricle. On this account the bend of the heart tube at the bulboventricular junction is effected toward the right side, turning its concavity to the left side, beneath the left layer of the dorsal mesocardium.

On the dorsal surface of the bulbus cordis there can be seen a triangular intermesocardial space, its plane is directed dorsally and slightly to the left. Its apex is directed caudally and at a lower level, where the demarcation between the bulbus cordis and ventricle wall show indefinitely. Its base is situated cranially and at a higher level, where the wall of the bulbus cordis is distinctly demarcated from that of the ventricle, and there marks the cranial termination of the dorsal mesocardium. Both at the apical and basal portions the lateral mesocardial layers come to fusion.

A single myocardial tube of the atria begins at the atrio-ventricular constriction cranially and continues into the sinus venosus caudally, demarcated by the sino-atrial constriction. This muscular tube shows a marked asymmetry on both sides, for the left side, being decidedly expanded in all directions in comparison with the right side, just contrary to the ventricle, in which the right side is apparently more voluminous than the left side and bulges considerably caudolaterally. Moreover, this opposing asymmetry must be attributed partly to the normal oblique direction of the atrioventricular constriction.

In consequence of this asymmetrical relation, the atrial tube forms a typical curvature with the ventricular limb at the atrio-ventricular junction, so that its convexity is directed toward the left side in the horizontal plane and ventralward in the vertical plane.

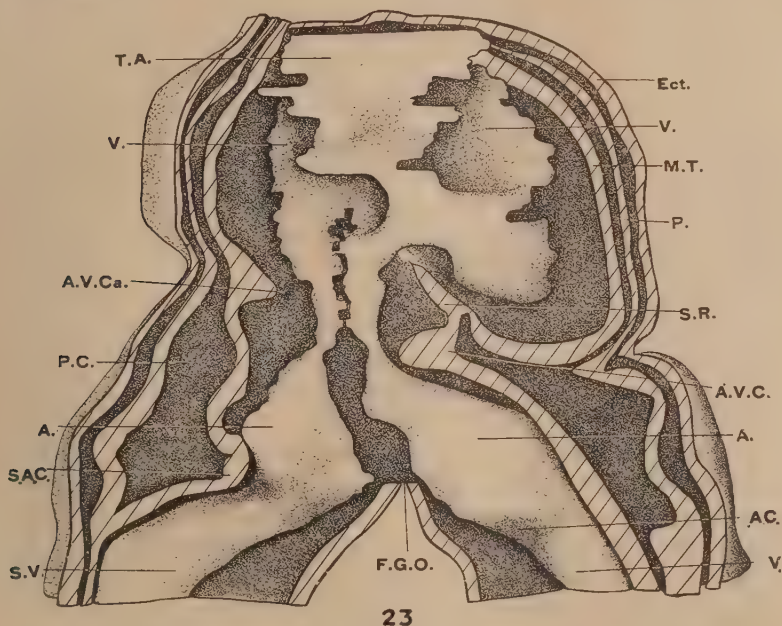


Fig. 23 Dorsal view of the reconstruction of the same embryonic shield (stage VIII) from which figure 22 was drawn. Dorsal wall of the pericardium and of the myocardium have been removed to expose the endothelium, which is subdivided into several individual portions in conformity with the myocardial subdivision. The two lateral endothelial tubes have fused and now communicate with each other throughout a middle third of the ventricle, but elsewhere they are separated. $\times 100$.

The cranial extremity of the atria opens into the left ventricle through the atrioventricular canal, which is situated on the left side from the midsagittal line, for the right atrioventricular constriction is apparently more deeply infolded and proportionately the prominent ridge at the inner wall is strongly pro-

jected into the canal on the right side. The caudal extremity of the atria is continued into the sinus venosus, which diverge from each other into the two lateral myocardial tubes in relation with the foregut opening. The demarcation of these different portions is indicated by the sino-atrial constriction, of which on the left side the myocardial wall is more deeply infolded than on the right side.

The two lateral layers of the dorsal mesocardium are fused together from a middle third of the ventricle to the cranial part of the atria; they are in close contiguity at the atrioventricular constriction, in which region the dorsal mesocardium is beginning to disappear in an embryo slightly older than that of this stage. But at the portion of the bulbus cordis and the caudal part of the atria, the layers of the dorsal mesocardium have not come in contact. The arterial opening is disposed nearly vertically, but slightly to the left side, through which the endothelial tube comes from the myocardial cavity, while the venous opening is disposed dorsocaudally and assumes an irregular triangular space. Its base is situated caudally and ventrally opposite to the foregut opening, as a result of which the layers of the dorsal mesocardium divert together with the corresponding muscular tubes, which continue caudally. Its apex of the venous opening is directed cranialward and lies at the higher horizontal level. Through this intermesocardial space the enclosed endothelial tube can be seen.

On the ventral surface the myocardium is reflected onto the ventral wall of the pericardium at the sinus venosus. Here it can be observed that the mesodermal cells have proliferated to form an appreciable thickening around the endothelial tubes, indicating the future septum transversum.

The lateral endothelial tubes are fused in the middle third of the ventricle to the extent of fifteen sections. In this part they communicate with each other and the endothelial cavity is considerably dilated (fig. 23). This craniomedian part of the endothelial tube is bifurcated into the two cranial horns and two caudal prolongations. The cranial horns extend symmetrically from the cranial wall for a short distance on both sides

and terminate blindly opposite to the cranial myocardial extremity of the ventricle, which is of conical form.

The right caudal prolongation is given off from the right side of its caudal wall and terminates as a short conical projection; its apical terminus is directed opposite to the caudal extremity of the right ventricle, conforming with it. The left caudal prolongation is given off from the left side of its caudal wall and caudally connects with the endothelial tubes of the atrium. These separate from each other and continue farther caudalward. From the origin of this left caudal prolongation caudally to the atrioventricular canal, that is, in the caudal part of the left ventricle, the two endothelial tubes show their smallest size and are very close in contact in some places, while in others they separate into two quite independent tubes with complete walls. Opposite to the atrioventricular canal the two endothelial tubes above mentioned begin definitely to separate into two lateral atrial endothelial tubes, increasing their calibers gradually caudalward, while they lie approximately in a parallel direction.

The caudal extremities of the atrial endothelial tubes continue immediately into the endothelial tubes of the sinus venosus and then into those of the vitelline veins. The transition from the atrial endothelial tubes into those of the sinus venosus is marked by a sudden diminution in their diameter together with the general decrease of their calibers and the abrupt lateral divergence of their course, due to the intervention of the foregut opening. These transitional points correspond to the external groove of the sino-atrial constriction.

In the ventricle the endothelial tubes are separated from the myocardial wall by a wide intervening space. In the atrium the intervening space becomes considerably narrower, and finally in the sinus venosus the endothelial tubes are enclosed intimately by their own independent myocardial wall, so that no appreciable space can be seen.

The endothelial tube of the bulbus cordis extends from the dorsal surface of the right ventricular endothelium as its continuous prolongation. This endothelial tube proceeds at first

dorsocranially and then slightly toward the left side. This is enclosed by the corresponding myocardial wall of the bulbus cordis, which is closed cranially, but caudally opens and communicates with the ventricular cavity, as already mentioned. The right ventricular endothelium, which gives off the endothelial tube of the bulbus cordis, is fused together with the left one, but the left part of the fused ventricular endothelium participates in no way with the bulbus cordis.

The endothelium of the truncus arteriosus continues farther dorsally and slightly toward the left side from the bulbus cordis and passes through the above-mentioned arterial opening, and then bifurcates into lateral symmetrical branches, which are located between the foregut floor and the lateral dorsal mesocardial layers and continue farther cranially into the ventral aortae.

The first aortic arch and the ventral aortae are completely formed and the dorsal aortae are considerably elongated caudward.

SUMMARY AND CONCLUSION

In our observations the first sign of the formation of angioblasts is shown in stage I, embryo A, in which neither the head fold nor the anlage of the pericardial cavity has yet appeared.

On the ventral surface of the mesoderm of the splanchnopleura of the cranial portion, cell bands first begin to separate, which separation is more advanced in the embryos B and C. These cell bands are regarded as angioblasts and they are frequently found to adhere to the indented and loosened mesoderm of the splanchnopleura by broader or narrower protoplasmic bridges. It has frequently been pointed out that mitotic figures are found in the mesoderm of the splanchnopleura in the neighborhood of angioblasts. Furthermore, in many cases where the angioblasts are in close contact with the mesoderm of the splanchnopleura, it is impossible to discriminate the angioblasts from the mesodermal cells of the splanchnopleura, as concerns their sizes, forms, staining reaction, and the form of the nuclei, while a great difference can readily be recognized between the angio-

blasts and the adjacent entodermal cells. These findings show that in the genetic origin the angioblasts for the future endocardium are derived directly from the mesoderm of the splanchnopleura. The origin of the angioblasts from the mesodermal cells continues until a later stage, in which the greater part of the endothelial tubes are already differentiated from the angioblasts in the anterior portion of the embryo, but the origin of the angioblasts can be recognized in the posterior part of the embryo, as is shown in the embryo of stage III.

In their well-known work on pericardial development, Strahl and Carius found it impossible to decide whether the embryonic coelom in the guinea pig appears at first in the region of the heart anlage, proceeding forward into the pericephalic mesoderm, or whether it begins first in the pericephalic mesoderm and then spreads out caudally. They speak as follows: "Doch können wir augenblicklich eine ganz sichere Entscheidung nicht geben." The cause of this ambiguity is that they began their investigation of the origin of the intraembryonic coelom at too late a stage.

For the dog, Bonnet states that, concerning the origin of the intraembryonic coelomic space, that the lateral pleuropericardial cavities, having already distinctly appeared, anticipate the formation of the pericephalic space. To quote Bonnet directly: "Eine ebensolche Spaltung des Mesoderms führt in VIII5 gleichzeitig im Bereiche des Herzwulstes zur Bildung der Pleuro-Pericardialhöhle. Ihre zuerst paarig angelegten spalten vergrößern sich, vereinigen sich nach vorne und bilden so ein nachhinten offenes Hufeisen; den pericephalen und lateralen Teil der Pleuro-Pericardialhöhle."

In our specimens, embryo C, stage I, shows the discontinuous formation of the intraembryonic coelomic spaces in the cranial portion of the embryonic shield, as also in the pericephalic mesoderm, these spaces beginning as multiple foci. But they are primarily absent in the middle portion of the pericephalic mesoderm.

In stage II, in which the head fold of the embryo begins to separate from the surrounding blastoderm and the foregut has

just begun to develop, the intraembryonic coelomic space spreads out cranially into the pericephalic mesoderm, cleaving the mesodermal layer in such a way, that the lateral primitive pericardial cavities communicate with each other. In a just slightly younger embryonic shield than this, each lateral pericardial cavity has progressed cranially into the pericephalic mesoderm, showing in this place a slit-like space, which however, is divided by a thin mesodermic bridge in the middle line.

The pericardial cavity, therefore, commences simultaneously in the multiple foci, separating irregularly by mesodermal bridges throughout the lateral plate in the cranial portion of the embryonic shield and in the pericephalic mesoderm. These multiple coelomic spaces become confluent to form a single pericardial cavity, having an inverted-U shape, when the mesodermal bridges at the middle line of the pericephalic mesoderm have ultimately disappeared and, in consequence, at this time the bilateral pericardial cavities, already widely confluent, communicate from side to side (stage II, A). In this embryonic shield relatively wide endothelial tubes are differentiated only in the region of the hindbrain plate, where the pericardial cavity is wide open and the mesoderm of the splanchnopleura is thickened, projecting into the pericardial cavity as a prominent fold. In the pericephalic portion of the mesoderm, however, the pericardial cavity is seen merely as a lineal cleavage. Here a few angioblasts are scattered between the slightly thicker mesoderm of the splanchnopleura and the underlying entoderm.

In stage III the bilateral myocardial folds become quite prominent, so that in the region of the hindbrain plate they have been almost converted into the myocardial tubes, and enclose the well-developed endothelial tubes.

The formation of these myocardial folds has progressed cranialward opposite to the foregut opening on the left side. At the same time the endothelial tube becomes gradually thinner cranialward and terminates slightly caudad to the foregut opening. On the right side the formation of the myocardial folds proceeds still farther cranially into the caudal part of the craniomedian limb of the pericardial cavity, where the thicker mesoderm of

the splanchnopleura is raised from the underlying entoderm and in the space between them a number of angioblasts are distributed. On the right side the endothelial tube terminates cranially just opposite to the foregut opening. In front of the cranial termination of the lateral endothelial tubes a number of angioblasts are scattered, so that the cranial extremities of the endothelial tubes are nearly connected with each other through these angioblasts.

The cranial extremities of the lateral myocardial folds have not yet come to complete confluence, as the mesoderm of the splanchnopleura, slightly cephalad to the cranial extremity of the left myocardial fold, remains still in loose contact with the underlying entoderm. If this portion of the mesoderm of the splanchnopleura were completely raised from the underlying entoderm, forming the myocardial fold, then the myocardial anlagen would come into confluence.

The most prevalent opinions with regard to the mode of the formation of the unilateral myocardial heart anlage from the bilateral myocardial tubes agree that, as above described, the bilateral myocardial tubes, at first independently, come to actual fusion with each other, and then the septal wall between them is absorbed secondarily, thus forming a single myocardial cavity. Our specimens show that the formation of the myocardial folds does not occur synchronously throughout the pericardial cavity, as in the region of the hindbrain plate they first appeared and developed considerably, while in the craniomedian limb of the pericardial cavity the formation of the myocardial folds was just starting and rising slightly from the underlying entoderm. However, the communication of the lateral myocardial tubes is accomplished when the formation of the myocardial folds is completed in the craniomedian limb of the pericardial cavity, in which region the formation of these folds occurs last. For this reason, the cranial prolongation of the lateral myocardial tubes has not been brought about by the direct extension of the first part of the myocardial tubes, but by the continuous progressive differentiation into the craniomedian limb of the pericardial cavity. Therefore, the confluence of

the myocardial tubes into a single myocardial cavity is not accomplished by the actual fusion of the bilateral myocardial tubes, followed by absorption of the septal walls.

In stage IV the formation of the myocardial fold is completely accomplished in the craniomedian limb of the pericardial cavity, elevating the mesoderm of the splanchnopleura from the underlying entoderm and projecting into the pericardial cavity. Both lateral myocardial tubes communicate with each other in this region.

Both the myocardial tubes are quite voluminous. They dilate in all directions, especially in their cranial portions, and they gradually reduce their dimensions caudalward. On the surface of these transitions no distinct demarcation can be noted.

The two lateral endothelial tubes are well developed, lying side by side together in the portion of the confluent myocardial cavity, and here independent, intermediate endothelial cells are scattered between the lateral endothelial tubes.

In stage V the cranial portions of the two lateral myocardial tubes show much more dilatation and elongation, as their extent from the foregut opening to the cranial extremities considerably increases. But their confluent part still remains short. The transition from the cranial dilated myocardial tubes to their caudal slender portions is marked by a distinct annular atrio-ventricular constriction, which appears clearly first in this embryo.

A number of workers declare that the lateral myocardial tubes are subdivided into many individual portions by the demarcations prior to the fusion of the lateral myocardial tubes; in the chick, Duval, '99; in the cat, Martin, '02; in the rabbit, Kölliker, '84. Kölliker states, "Ein Herz aus diesem Stadium ist sehr verschieden von dem primitiven Herzen eines Hühnerembryo, was einfach darin begründet ist, dass, wie bemerkt, bei Säugethieren schon vor der Verschmelzung der beiden Herzhälften die drei Herzabschnitte angelegt sind."

Mollier declares in similar language: "An den beiden Herzhöhlen ist aber kurz vor ihrer Vereinigung schon eine Gliederung bemerkbar."

In our specimens this embryo shows first the atrioventricular constriction, even though in the previous embryo two myocardial tubes were already confluent into a single myocardial cavity.

The two lateral endothelial tubes are considerably developed, especially in the confluent portion of the myocardial cavity, where they approach each other almost to contact. From the atrioventricular constriction caudalward the two endothelial tubes assume an abruptly narrow caliber, thus distinguishing the larger cranial ventricular from the smaller caudal atrial portion. In tracing farther caudally, no demarcation can be detected on them.

In stage VI the confluent myocardial cavity increases especially in the craniocaudal extent. The cause of this may be attributed partly to the retirement of the wedge-shaped septal ridge cranialward, which had projected into the confluent myocardial cavity, as the conversion of the inner walls of the cranial lateral myocardial extremities, and partly to the active backward progress of the foregut opening. Approximately, in the whole extent of the ventricle and in the cranial part of the atria the two lateral myocardial cavities communicate with each other and these two myocardial portions are demarcated sharply by the atrioventricular constriction. In the middle third of the ventricle the two lateral endothelial tubes are actually fused and communicate with each other for a short distance. At the atrioventricular constriction the calibers of the two endothelial tubes are considerably reduced and, as we proceed still farther caudally, they are again gradually increased in diameter.

In an embryo of *Perameles nasuta* having fifteen to sixteen somites, Miss Parker pointed out that the fusion of the lateral endothelial tubes first took place. The fused portion already extends throughout about eighteen sections. She states that from this portion the *bulbus cordis* is derived.

Wang reports concerning a ferret embryo, having thirteen to fourteen somites, that the two endothelial tubes had united in a part of their extent. The fused portion, extending throughout about sixteen sections, appeared to be the ventricular part.

In our specimens this embryo shows first the fusion of the two lateral endothelial tubes throughout only seven sections, having a $5\ \mu$ thickness, and this united part corresponds to a middle third of the ventricle and lies precisely on the midsagittal plane. In the guinea pig the fusion of the lateral endothelial tubes takes place at a relatively early stage of development—a stage in which in the myocardial and endothelial tubes there can be distinguished simply the ventricular and atrial portions. In the above-mentioned animals investigated by other authors, the fusion of the lateral endothelial tubes was first noted in the relatively older embryo, in which the different parts of the myocardial and endothelial tubes are already definitely subdivided. Moreover, their embryos show that the fused portion is considerably extended in comparison with this embryonic shield.

The factors which are generally accepted as the cause of the loop formation of the endothelial tubes depend on the fact that the rate of growth of the two endothelial tubes exceeds that of the pleuropericardial cavity. Bonnet depicts a dog embryo in which the primary subdivision of the endothelial tubes into sinus venosus, atrium, and ventricle has occurred before they have fused to form a single myocardial cavity.

Wang pointed out the loop formation with the subdivision of the heart (atrium, ventricle, bulbus, etc.) in the ferret embryo, before the endothelial tubes had become fused.

But in our specimens there is no loop formation, nor can the subdivision of the heart be marked out on either of the endothelial tubes before they are fused together, even though the ventricle and atrium may be roughly distinguished by their difference in size.

Contrary to the above-mentioned assumption that the loop formation of the endothelial tubes has been brought about, the moment of fusion of the two lateral endothelial tubes shows quite other facts in the guinea pig. In the embryonic shield at this stage of development the confluent part of the myocardial tube grows excessively in the craniocaudal direction and decreases its lateral width in comparison with the embryo of stage V, as measured and compared on both reconstruction

models which had been magnified to the same degree. Consequently, the two endothelial tubes are brought together in the median plane, where they come to fusion, by the extreme longitudinal stretching of that part of the myocardial tube in which the endothelial tubes are enclosed. Concurrently, the active dilatation of the two endothelial tubes plays a part in bringing about the fusion, which takes place first in the most dilated portions.

In stage VII the myocardium presents cranially a single expanded craniomedian extremity, assuming a sac form, and here represents the ventricle, while caudally this myocardial sac is bifurcated into two rather slender myocardial prolongations. Their demarcation is indicated by the well-developed atrioventricular constriction slightly cephalad to the foregut opening. The transition from the atrium into the sinus venosus is marked by an indefinite indentation on the bilateral myocardial tubes caudad to the foregut opening and slightly more distinct on the left side. Corresponding to these myocardial constrictions, there can be pointed out a similar indentation on the endothelial tube on the left side.

The two lateral endothelial tubes are fused together in the cranial two-thirds of the ventricle, and its cranial extremity is terminated as a single conical apex opposite to the cranial end of the myocardial ventricle. In tracing farther caudalward from this united portion, the two endothelial tubes are separated.

In this stage of the development the myocardial and endothelial heart anlagen of the ventricle present a considerable asymmetry, due to the unequal growth of the individual parts, despite the fact that, in the embryonic shields prior to this stage of development, the heart anlagen are shown as a practically symmetrical development on both sides, even after the fusion of the lateral endothelial tubes has already been accomplished.

Miss Parker describes the heart of the *Perameles obesula* stage V as follows: "In the ventricular region of the heart, the right and left endothelial tubes are approximately equal in size, but where there is an inequality the right is the larger."

In the ferret embryo Doctor Wang says: "It has been found that the two tubes, prior to fusion, appear to have been shifted as a whole toward the right side and that they remain in this position even after partial fusion has taken place."

In our specimens the myocardial asymmetry of the ventricle is attributed partly to the extraordinary bulging of its right wall dorsally, laterally, and slightly caudally, and partly to the deeper infolding of the myocardial wall of the atrioventricular constriction of the right side. In the ventricle the endothelial tubes are much more dilated on the right side than on the left throughout its whole length, regardless of the fused or non-fused portions, and it expands considerably dorsally, laterally, and caudally. Consequently, they deviate from the middle plane toward the right side and are situated more to the right side of the myocardial ventricle. The right endothelial tube is elongated dorsally at the caudal third of the ventricle, where the two lateral endothelial tubes, being separated, pass through the intermesocardial space vertically. From this portion the bulbus cordis develops in a later stage; its termination is cranially bifurcated into two lateral endothelial branches, which continue farther cranialward into the ventral aortae.

In stage VIII there are present three distinct constrictions on the tubular myocardial surface, infolding the whole thickness of the myocardial wall into the myocardial cavity. Consequently, the myocardium can be subdivided by very distinct demarcations into the bulbus cordis, bulboventricular constriction, ventricle, atrioventricular constriction, atrium, sino-atrial constriction, and sinus venosus in the craniocaudal succession.

The bulbus cordis is demarcated from the dorsal wall of the expanded right ventricle at its cranial end by the horizontal bulboventricular constriction. The bulboventricular constriction shows considerable asymmetry, making a deeper furrow on the external surface of the myocardium at the left and cranial sides, while at the right side it is present as a shallow depression on the external surface, diminishing imperceptibly caudalward, until it has entirely disappeared at the part of the right ventricle. Thus neither external furrow

nor infolding of the myocardium is shown along the caudal boundary of the bulboventricular junction, and here the wall of the bulbus is directly continuous into that of the right ventricle. Corresponding to the external view, the deep infolding of the myocardial wall as the inner prominent ridge is shown at the left and cranial sides of the bulboventricular canal, while on the right side it can be recognized only cranially and disappears insensibly caudalward. In this fashion the curvature of the myocardium at the bulboventricular junction is effected in such a way that its convexity is turned toward the right side. On the dorsal aspect of the bulbus cordis there is a triangular intermesocardial space disposed vertically and slightly toward the left side, through which the truncus arteriosus passes out from the myocardial cavity up to the floor of the foregut.

The atrioventricular canal is well marked and is disposed approximately in the vertical plane. It is produced by the infolding of the myocardial wall, which is deeper and more caudad on the right side than on the left. Consequently, the opening of this canal is situated on the left side of the middle plane. In this relation the myocardial tube forms a marked curvature at the atrioventricular junction, turning its convexity toward the left side and ventralward, with the result that the ventricular portion lies at the right side and slightly ventrally to the atrial portion. This curvature is remarkably accentuated in the next stage of the development, in which, for a short extent, the dorsal mesocardium disappears at the atrioventricular junction and herewith the ventricle comes to the ventral surface of the atrium, being free from the restriction of the dorsal mesocardium.

The ventricle can be divided incompletely into two limbs by the ventral and dorsal longitudinal sulci. At the caudal part of the ventricle, for a short distance, the two limbs are divided into two completely independent cavities by the septal wall. The caudal extremity of the right ventricle terminates blindly as a conical process and it projects caudolaterally.

In the literature I could not find a description of this. On first observation it seemed to me that the septal wall and its conversion into prominent ridges at the inner surface of the ventral and dorsal myocardial wall were produced by the actual fusion of the two lateral myocardial tubes. Therefore, this may account for the remnant of the primitive myocardial septum. But in the embryos of stages VI and VII there was present no septal wall nor prominent ridge similar to this in their single ventricle, in which they would be more distinctly present if they accounted for the production of the actual fusion of the lateral myocardial tubes and the remnant of the primitive cardiac septum.

Accordingly, it appears to be due to the fact that the caudal surface of the myocardial ventricle on the right side is projected actively backward by the unequally excessive rate of growth in this portion, while in the middle plane a part of the myocardial wall does not proportionately accompany this active backward growth, but remains as the septal wall.

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Posición anormal del duodeno.

En el caso descrito por el autor, el duodeno presentaba próximamente la longitud normal, pero estaba plegado de un modo anormal a la derecha de la raíz del mesenterio, delante del riñón. La porción superior es completamente normal. La porción descendente desciende al principio pero después gira dorsalmente delante del hilus del riñón para unirse con un asa semejante de la porción que normalmente forma el segmento transverso. Este último está situado más caudalmente, enfrente del polo inferior del riñón, y su porción terminal corta pasa transversalmente detrás de las raíces de los grandes vasos mesentéricos, a la izquierda de los cuales se une con el yeyuno. Esta unión está situada a la derecha de la columna vertebral, pues la raíz del mesenterio está en el territorio del lado derecho. Las asas anormales del duodeno están insertas delante del riñón mediante el peritoneo. La cabeza del páncreas se extiende inferiormente en el lado mesial a las asas duodenales. El extremo izquierdo del colon transversal forma una larga asa dirigida hacia abajo. El colon ascendente es más largo que lo normal, y el ciego y el apéndice constituyen el contenido de una hernia inguinal oblicua. El autor interpreta el presente caso como un caso de rotación interrumpida o formación incompleta de la curvatura duodenal en el embrión. Veinte casos diferentes de malposición del duodeno han sido citados en la literatura y todos ellos ilustran de uno u otro modo el mismo principio.

Translation by José F. Nonidez
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ABNORMAL POSITION OF THE DUODENUM

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SEVEN FIGURES (TWO PLATES)

This case is reported because it shows a rare malposition of the duodenum and is an example of incomplete rotation of this organ around the mesenteric pedicle. There are not many cases of malposition of the duodenum on record. The surgical importance of these anomalies is indicated in the case reported by Mumford ('06) and that reported by Freeman ('20). These cases are of interest because they can be explained on the basis of arrest or variation in the normal developmental processes in that region.

The position of the duodenum in the adult has been studied by many anatomists and surgeons, among whom may be mentioned Braune, Treves, Jonnesco, Schiefferdecker, Dwight, Cunningham, and Ochsner. Dwight ('96-'97) made an extensive study of its shape. Addison ('01) has made an extensive study of the variations of its position.

Meckel, in 1917, and His, in 1885, established the development of the intestinal canal. Mall ('97) has demonstrated how the coils of the intestine develop and the position which they ultimately assume. A comprehensive study of the subject is given by Lewis ('12). Lewis and Papez, in a series of reconstructions designed to show the development of the mesentery, demonstrated how the duodenum rotates around the mesenteric pedicle in young human embryos. More recently, Frazier ('19) has figured a series of reconstructions to show the formation of the duodenal curve, and Vogt ('20) has figured the duodenum and structures in the mesenteric pedicle in human embryos 12.5, 22, and 33 mm. long.

Several embryonic structures shape the duodenal curve. In the young human embryo the mesenteric pedicle is formed dorsal to the gastroduodenal region by the primitive portal anastomosis, the pancreas, and the roots of the mesenteric vessels. At an early stage (5 mm.) the primitive portal anastomosis, the proximal ends of the vitelline vessels, and the hepatic bud form the conspicuous features in this region. Soon, however, the growing pancreas invades this area of the mesentery and forms a constant and prominent mass around the roots of the great mesenteric vessels. It is over the right side of this pedicle that the curve of the duodenum is begun, and is subsequently completed by passing around its dorsal side. Complete rotation of the duodenum is normally concomitant with the rotation of the general mesentery, as shown in a 42-mm. embryo by Papez and Lewis ('17) and in a 40-mm. embryo by Frazier ('19).

REPORT OF CASE

The case (fig. 1) described in this report probably illustrates an arrested or incomplete rotation of the duodenum as observed in an adult male subject (no. 607) in the anatomical laboratory of Cornell University at Ithaca, New York. The viscera of this subject had a healthy appearance and there was a complete absence of inflammatory adhesions. The position, relations, and peritoneal attachments of the duodenum must be regarded as having an embryonic origin.

The stomach was somewhat smaller than normal, but its position, relations, and peritoneal attachments were quite normal. The pylorus had the usual situation just to the right of the midline. There was no shortening of the lesser omentum. No adhesions of the pylorus or duodenum to the liver were present. The case reported by Brash and Stewart ('20) is cited here to show that a reversal of rotation of the stomach and mesogastrium (to the right) produces a marked malposition and flexion of the duodenum, but is not necessarily associated with complete reversion or torsion of the mesentery and intestines. They cite similar cases of transposition of the stomach reported by Lunay

and by Debouie in which the three parts of the duodenum were reported as normal. In the case reported by Bryce ('99) there was a marked constriction of the stomach which he thought might have a causal relation to the duodenal anomaly.

The liver was quite normal excepting that the tip of the left lobe (*e*) was elongated and constricted from the main portion, comparable to the liver described by Harman ('99) in which there was no mention of variations of the duodenum. Since this anomaly of the liver is one often observed, it would not seem to have any causal relation to the malposition of the duodenum. The gall bladder, bile ducts, and other structures in the lesser omentum had the usual disposition.

The duodenum was wholly to the right of the midline coiled in an unusual manner in front of the hilus and lower pole of the right kidney. Its length was about normal. Its superior portion (*sd*) formed a coil convex upward, and had normal relations. Its superior surface was in contact with the quadrate lobe of the liver; it was covered by peritoneum which passed to the left into the epiploic foramen and peritoneum of the lesser omentum and passed downward into the superior layer of the mesocolon. Its left surface lay against the upper portion of the head of the pancreas and against the hepatic artery. Thus, the hepatic fold (inferior pancreaticoduodenal fold) passed along the upper left border of this portion of the duodenum. The hepatoduodenal ligament was attached to the duodenum just to the right of this fold. The gastroduodenal artery passed downward behind the duodenum.

The descending portion of the duodenum formed a coil (*dd*) which turned upward to join a coil of the inferior portion in front of the hilus of the right kidney. The upper and right surfaces of the descending coil were in relation with the inferior surface of the gall bladder and right lobe of the liver. They were covered by peritoneum which passed dorsally to the surface of the right kidney and ventrally into the upper layer of the transverse mesocolon. The left surface lay against the head of the pancreas, common bile duct, and upper extent of the superior mesenteric vessels which separated it from the inferior vena

cava. In front and along the lower border of these duodenal coils passed the right extremity of the transverse colon bound to them by the mesocolon. These coils of the duodenum rested in part upon the right end of the transverse colon. The accessory pancreatic duct could not be located. The duodenal papilla with the openings of the common bile duct and the main pancreatic duct was situated in the dorsomedial wall of the descending coil (*dd*). No duodenal diverticula were found.

The head of the pancreas (*pa*) was molded against the left side of the descending coil (*dd*) and extended for some distance in a caudal direction to the right of the great mesenteric vessels. The pancreaticoduodenal vessels had the usual distribution between the head of the pancreas (*pa*) and descending coil (*dd*).

The third portion of the duodenum (*td*) formed a large upward coil in front of the hilus and lower pole of the right kidney. The ascending end of the coil passed dorsal to the root of the great mesenteric vessels and head of the pancreas to gain the left side of the root of the mesentery where it turned down to join the jejunum (*jj*). This junction (*jj*) was in front of the right psoas muscle to the right of the inferior vena cava opposite the third lumbar vertebra. The coils were covered on the right side by peritoneum which bound them to the surface of the right kidney and to the right parietal wall. The terminal portion as it passed through the root of the mesentery received from it the usual covering. Ventral to the terminal portion was the root of the mesentery (*mes*) with the superior mesenteric vessels and head of the pancreas (*pa*). Ventral to these was the right end of the transverse mesocolon.

The abnormal coiling of the duodenum to the right of the root of the great mesenteric vessels and the right-sided position of the mesentery and duodenojejunal junction were the striking features of this anomaly. They are to be interpreted as being due to an incomplete rotation of the duodenum around the mesenteric pedicle in the embryo.

The root of the mesentery of the small intestine and its usual contents extended along the right surface of the right psoas into the iliac fossa. Its upper extent was about 7 cm. to the

right of the midline. The lower end was elongated and permitted a considerable downward displacement of the ileocaecal junction and caecum which with the appendix formed a large oblique inguinal hernia.

The colon was longer than usual. The left portion of the transverse colon formed a large downward loop in the great omentum. The ascending colon was so elongated as to permit the caecum and appendix to enter the large hernia. In the duodenal anomaly figured by Harman ('98) there was a large downward loop of the ascending colon at the hepatic flexure. It might appear that an overgrowth of the colon with an exaggeration of the torsion of the entire tract may have a causal relation to such duodenal anomalies. However, in Sencert's ('05) case there was an incomplete growth as well as incomplete rotation of the intestinal tract, the caecum remaining in the left hypochondrium. In the case reported by Armstrong ('10) and in Boyd's ('14) case similar conditions obtained.

ABSTRACTS OF REPORTED CASES

In 1886 Schiefferdecker reported two cases in which there was an unusual coiling of the duodenum and first portion of the jejunum in the root of the mesentery.

In 1896 Dwight referred to some curious cases he had seen in which the distal part of the duodenum formed a coil in front of the left kidney, so that the duodenum had the shape of an S placed on its side. His cases were explained as due to an overlong duodenum (Piersol's Anatomy).

Roud, in 1898, reported a case (fig. 6) in an adult in which the first portion of the duodenum was normal, but the remainder suspended in a short mesoduodenum extended downward to the right iliac fossa and did not cross dorsal to the mesenteric vessels. The caecum was in the pelvis. Ascending over the right pelvic brim the colon passed to the left through the root of the mesentery. He recognized that the condition was an anomaly of embryonic origin in which the normal torsion of the intestines had been partially reversed so that the colon passed behind the mesentery of the small intestine.

Harman, in 1898, reported a case (fig. 4) in which there was a coiling of the descending portion of the duodenum and the duodenojejunal junction was to the right of the second lumbar vertebra and turned to the right. This is comparable to case 5 reported by Addison. There was also a large downward loop of the colon at the hepatic flexure, as if it were double. Harman's ('98) case is comparable to the one reported in this paper.

Bryce, in 1899, reported a case (fig. 2) in which the first portion of the duodenum was normal, but the second and third portions formed a long downward U-shaped loop attached in front of the right kidney and to the right of the great mesenteric vessels. The short terminal portion passed dorsal to the mesenteric vessels and joined the jejunum opposite the second lumbar vertebra. There was a marked constriction of the stomach. Bryce ('99) thought that the duodenal anomaly might have been produced by a failure of the normal twisting of the duodenum (Young, '98).

Addison, in 1901, reported a case (no. 40) in which the ascending portion was dorsal and somewhat to the right of the descending portion, comparable to Bryce's case (fig. 2). In another case (his no. 7) Addison found the duodenum and the duodenojejunal junction to the right of the midline.

Fawcett and Blachford, in 1904, made 337 postmortem examinations to determine the position of the third part of the duodenum. In four cases the duodenum did not cross the vertebral column, but ran into the rest of the intestine along the right side of the column. From their observations it would seem that this anomaly occurs in more than 1 per cent of individuals.

Sencert, in 1905, reported a case (compare with fig. 5) of incomplete torsion of intestinal loop in a newborn child. The duodenum and head of the pancreas were contained in a short mesentery and were movable. The duodenum was on the right side, formed a simple curve; and its third and fourth portions were absent. The colon was not fully developed; the caecum was in the left hypochondrium. The root of the mesentery was adherent along the midline, as in Eddy's case (fig. 3).

The case (fig. 7) reported by Clermont ('05) was singular in that the first and second portions of the duodenum were to the left of the superior mesenteric vessels, while the transverse and ascending portions were on the right. As in other cases, the terminal portion was short and passed dorsal to the great mesenteric vessels to join the jejunum. In this case it appears that there was a partial reversal to the left of the normal duodenal loop.

Mumford, in 1906, did a gastrojejunostomy on a case (compare with fig. 4) in which there was an incomplete formation of the duodenal curve. The duodenojejunal junction was so far to the right that, as the stomach filled, it pulled away from the jejunum at the site of the operative union. He emphasizes the importance of recognizing such anomalies.

Reid, in 1908, reported an incomplete torsion (fig. 5) of the intestinal loop. In his case the whole colon, quite fully formed in length, remained on the left side. The duodenum was unusually mobile. It was coiled on the right side of the great mesenteric vessels and there joined the jejunum.

Armstrong, in 1910, reported a case (compare with figs. 5 and 6) in which the duodenum extended to the right of the hepatic flexure and ascending colon, and joined the jejunum below the caecum. With the head of the pancreas it was suspended in a fairly long mesentery. "The condition was clearly one of arrested development."

Eddy, in 1912, reported a case (fig. 3) in which the duodenum was comparable to the case reported by Reid. Although the caecum was in the right iliac fossa, the larger part of the colon was on the left side. In this case the rotation of the primitive loop of gut was arrested, so that the intestine persisted in its primitive relation. The pancreas consisted of two parts.

Boyd ('14) reports a case (compare with figs. 5 and 6) in which the third and fourth portions of the duodenum were absent. The duodenum joined the jejunum under the hepatic flexure of the colon. The jejunum commenced as coils on the right side and extended into the right iliac fossa.

Freeman ('20) reported a case (compare with fig. 2) of a long U-shaped duodenum with a kink and a constriction at the duodenojejunal junction.

Brash and Stewart ('20) reported a case of right-sided rotation of the stomach, spleen, and mesogastrium in which the normal duodenal curve was markedly altered (compare with fig. 7).

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ABBREVIATIONS

<i>a c</i> , ascending colon	<i>mes</i> , mesentery
<i>a d</i> , ascending duodenum	<i>m d</i> , mesoduodenum
<i>b d</i> , bile duct	<i>o b</i> , omental bursa
<i>c l</i> , colic ligaments	<i>pa</i> , pancreas
<i>d c</i> , descending colon	<i>py</i> , pylorus
<i>d d</i> , descending duodenum	<i>s d</i> , superior duodenum
<i>e</i> , tip of left lobe	<i>s m v</i> , superior mesenteric vessels
<i>g b</i> , gall bladder	<i>st</i> , stomach
<i>i v c</i> , inferior vena cava	<i>t c</i> , transverse colon
<i>j j</i> , jejunal junction	<i>t d</i> , transverse duodenum

PLATE 1

EXPLANATION OF FIGURE

1 Abnormal position of the duodenum in an adult man. The coiling of the descending and transverse portions in front of the kidney are the chief features. The root of the mesentery was on the right side.

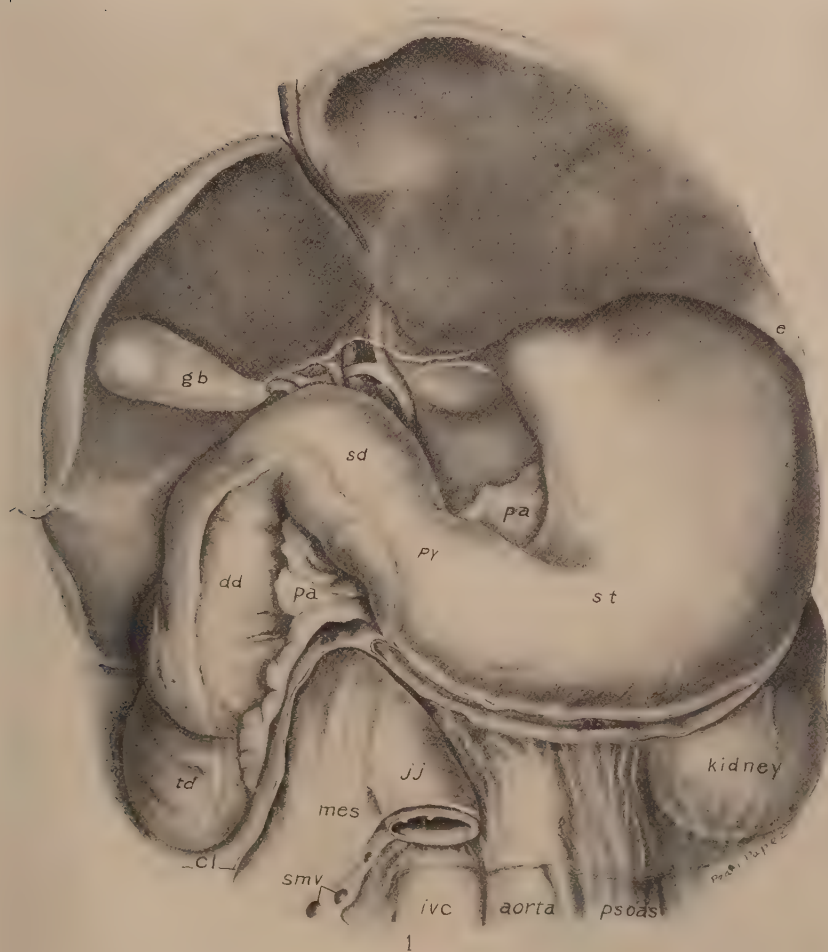
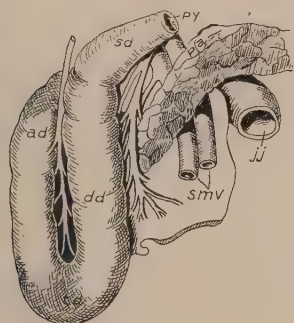


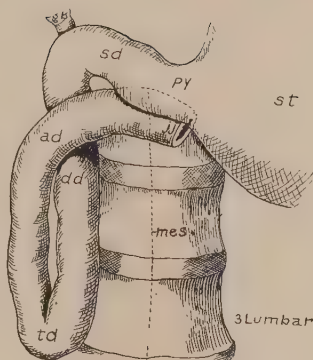
PLATE 2

EXPLANATION OF FIGURES

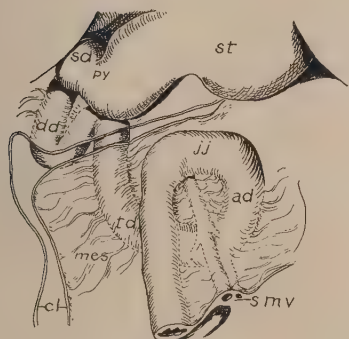
- 2 Copy of Bryce's case. Freeman's case was similar, but the ascending limb of the U was to the left as in U forms described by Dwight.
- 3 Copy of Eddy's case. Compare with figures 5 and 6.
- 4 Copy of Harman's case. Mumford's case was similar.
- 5 Copy of Reid's case. Boyd's case was similar. Sencert's case in a newly born child was similar, but caecum was in left hypochondrium.
- 6 Copy of Roud's case. Armstrong's case was similar. Both resemble cases included in figure 5.
- 7 Copy of Clermont's singular case. The case of Brash and Stewart was similar, but stomach, spleen, and mesogastrium were rotated to the right.



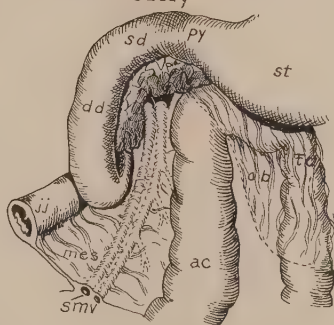
2 Bryce



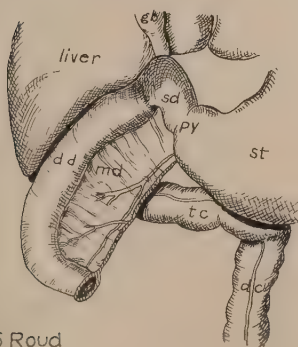
3 Eddy



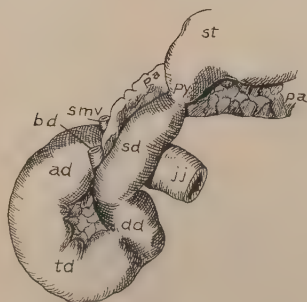
4 Harman



5 Reid



6 Roud



7 Clermont

Resumen por el autor, Wesley M. Baldwin,
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Un estudio sobre la profundidad de penetración de la energía los
rayos de luz ultravioleta en el embrión del renacuajo.

En la presente investigación el autor ha descubierto que la luz de rayos ultravioleta de una longitud de onda comprendida entre 214.4 y 240.5 $\mu\mu$ tiene tan solo un poder de penetración de 0.02 mm. en el embrión del renacuajo. Toda la energía, en otras palabras, es absorbida por las dos capas de células ectodérmicas de los embriones durante el periodo de oclusión del tubo neural. La energía luminosa produce una reacción intracelular caracterizada por una ausencia de fenómenos vasculares de inflamación, por esferulación de las células y retardamiento del proceso de reparación, sin ir acompañados de extrusión o exfoliación.

Translation by José F. Nonidez
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A STUDY ON THE DEPTH OF PENETRATION OF ULTRAVIOLET LIGHT RAY ENERGY IN THE EMBRYO OF THE TADPOLE

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The author has previously detailed the effects of ultraviolet light ray energy acting upon the frogs' fertilized ovum during the early stages of development.¹ It was the purpose of the experiment to ascertain the localization of the organ-forming substances in the egg and incidentally the penetrative capacity of the rays. It is no new fact to point out in connection with the latter that radiant energy of this wave length is comparatively slightly penetrative. Henri² has measured the absorption capacity for wave lengths varying from 214.4 to 240.5 μ , and ascertained that protoplasm absorbed nine-tenths of the energy with thickness of 3.8 μ and 79.0 μ , respectively. The apparatus used for the experiments and described in the previous papers furnished a wide range of these wave lengths. The observed results seemed to indicate that only a relatively small mass of protoplasm superficially placed in the egg was so chemically altered by the energy as to be unable to participate in the normal developmental changes of the embryo. While it was difficult to ascertain the exact depth of penetration of the rays, the fact seemed to be demonstrable that the lethal action was restricted to a depth certainly no greater than 0.1 mm.

A more extended study of the action of the rays was carried out subsequently upon embryos of the tadpole in more advanced stages of development for the express purpose of determining

¹ Baldwin, *Anatomical Record*, vol. 9, no. 5, May, 1915, and *Biological Bulletin*, vol. 37, no. 5, November, 1919.

² v. Henri, Des Bancelis, and Wuermsier, 1912, "Etude de photochimie biologiques," Paris: Masson.

in terms of cell layers the depth of active penetration of the rays. A further desideratum consisted of the possibility of elimination of a certain error of absorption through the complete removal of the egg envelopes and of their investing jelly which had proved to be fluorescent and highly absorptive of light energy. The embryos which were used were selected at the time of closure of the neural tube. Several series of embryos served as controls for each experiment. About 100 specimens were rayed, of which thirty were sectioned serially and carefully studied. The localization of the activity of the rays was effected through the interposition of a tinfoil diaphragm between the specimen and the arc emitting the rays. A pinhole in the diaphragm permitted a beam of light 0.3 mm. in diameter to impinge upon the surface of the embryos. The intensity of the light was increased through the employment of two powerful quartz convex lenses placed close to the arc. The exposure time varied with the experiments. In all instances, however, it was continued until a whitish spot made its appearance upon the embryo; in other words, until the pigmented ectoderm became distinctly blanched.

An exposure prolonged beyond this characteristic reaction resulted in the production of a marked and sharply delimited swelling rapidly assuming globular proportions which in the course of a few hours was followed by an exovation. The specimens were afterward fixed according to Schultze's formalin method at periods ranging from fifteen minutes to thirty-four days after the exposure.

Microscopic examination of the sections demonstrated beyond question that the ultraviolet light rays had produced an injury which was wholly confined to the two-layered ectoderm of the embryo. The underlying mesodermal cells were normal in every respect. Upon careful measurement, the normal ectoderm was found to have a thickness averaging about 0.02 mm. over the region rayed. The absorption capacity of these superficial cells for the energy was sufficient to effectively protect the underlying mesodermal cells from the injurious action of those rays which filtered through them.

It would seem from the data given that, while diverse results are obtained through the use of this energy, these are referable chiefly to effects produced in and restricted to the superficial layers of the embryo. This is admittedly no new contribution to our knowledge on the subject, yet here is obviously demonstrable evidence of the complete absorption of practically all of the injury-producing energy by a thin two-cell layer of ectoderm with the concomitant protection afforded to the underlying cells by this procedure. The dosage gives an indication, moreover, of what might be termed the absorption capacity of the ectodermal cells compatible with their physiologic activity. A slight increase either in the time of exposure or in the concentration of the rays, the raying distance remaining constant, would have induced the death of the constituent cells. This was repeatedly verified during the experiments.

Again, it is difficult to deny that some of the more penetrative or 'harder' rays of physiologic activity must have reached the underlying mesodermal cells, yet the absence of morphologic modification and the want of evidence of developmental interruption among the cells of the mesoderm and of its derivatives both seem to argue the presence of so small an amount of this energy as not sufficiently potent to leave even a temporary indication of its reaction effect. In this connection it may be well to point out the capacity of the organism to rectify by means of a delayed process of chemical postgeneration whatever change may have been brought about by this form of energy such as was referred to in the before-mentioned earlier papers.

Several interesting phenomena of reaction are evidenced by these superficial cells. A temporary retraction of the chromatophores of the ectoderm, which accounts for the blanching results noted at the time of the experiment, is first manifested. This is followed within an hour by a marked distention of all of the cellular constituents of the ectoderm. This reaction is wholly confined to the cells of the ectoderm and is unaccompanied by the usual picture of blood-cell multiplication or vascular reaction. At the early stages selected for the experiment,

such a phenomenon is naturally accounted for through the absence during such periods of formed blood-elements and of peripheral vessels. No evidence could be obtained at any period following the raying that the maximum reaction was confined to the superficial layer of the ectoderm. So far as the histologic features might serve as a criterion, this was in both layers the same in kind and in degree.

Within this area the ectoderm was increased in thickness to three times that of the controls. A low swelling of uniform height was evident, consequently, in the gross. Histologic sections revealed an extension of this swelling as a downgrowth into the underlying mesodermal tissue. The increase in thickness depended upon two factors; first, an increase in size of the individual cytologic elements, and, secondly, an increase in number of these elements. The cells presented enlarged nuclei and cell bodies. Since the shape of the latter tended toward the spherular, there was a consequent loss of intimate contact between contiguous cell borders. The appearance resembled the phenomenon of cell retraction, and in exaggerated instances led to the formation of continuous, tunnel-like spaces which extended relatively great distances between the ectodermal cells. Such have been noted before by investigators studying the biological effects of radiant energy and, by the author as well, with x-rays. The assumption of the spherical outline suggests parenthetically that this feature might well be accounted for on the basis of a disturbance in surface tension of the cells induced by the light energy.

The quantity of pigment, normally restricted for the most part to the superficial surface of the superficial layer of cells of the ectoderm, was found to be greatly increased not only at this usual level, but throughout the entire thickness of the superficial cells and greatly increased in amount relatively in the cells constituting the deeper layer of the ectoderm (sunburn?). The cells of the injured area abandoned their orderly stratified appearance and assumed a heaped-up disorderly arrangement. In the thicker portions of the area as many as five or six irregular layers of these cells could be made out. Such appearances

obtained within twenty-four hours and were observed as late as thirty-days following the raying. Mitoses appeared frequently in the affected area after the first ten-day period, but at no time could amitotic division of cells be identified, thus confirming Poynter's observations on wound repair in embryos.³

Resolution was unaccompanied by vascular reaction at all periods of the process. The cells resumed their normal morphologic features gradually. The normal, orderly, stratified arrangement in cell layers was very gradually resumed by a process not at all clearly understood at the present time. Neither exfoliation of cells nor the features of cytolysis were at any time evident. Protoplasmic or nuclear extrusions were not detected. Whatever change had been artificially wrought appeared to be of the nature of an intracellular reaction, and as such would seem to be comparable to that brought about by x-rays. A lethal amount of energy had not been absorbed apparently by any cytologic constituent to so great a degree as to render it unfit for the subsequent chemical ontogeny of the cell. The damage was repaired by the cells as individuals and not by the cell mass as a whole. There was no interposition of a repair process on the part of the organism. The protraction of the restorative process is, furthermore, strongly reminiscent of the effects both of x-ray and of radium energy.

³ Poynter, *Anatomical Record*, vol. 16, no. 1, March 20, 1919.

Resumen por el autor, Emanuel Blankfein,
New York University.

Un ejemplo de disociación de las ramas de la arteria femoral profunda.

En el caso descrito por el autor la arteria circunfleja media se origina en una rama de la femoral que forma un tallo de origen común para ella y para las arterias perforantes primera y segunda. Las arterias perforantes tercera y cuarta también nacen de un tallo común, mientras que la circunfleja lateral nace independientemente de la femoral. Esta disposición de vasos que ordinariamente porceden de la arteria profunda no parece haber sido descrita previamente, aun cuando se han publicado tres casos algo semejantes.

Translation by José F. Nonidez
Cornell Medical College, New York

AN EXAMPLE OF DISSOCIATION OF THE BRANCHES OF THE A. PROFUNDA FEMORIS

E. BLANKFEIN

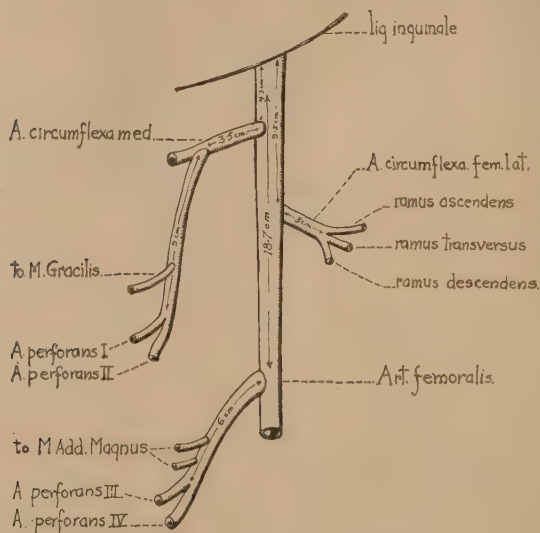
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New York University*

Although the circumflex arteries often fail to take origin from the profunda in accordance with the traditionally accepted description, the perforating arteries very seldom do so. Three cases are recorded in the literature in which the aa. perforantes have not arisen from a profunda artery of the usual type, and a fourth example of the anomaly has come recently under observation. The arrangement of the perforating arteries of the case in question differs from that of the cases already published, which differ also from one another. This fourth case, therefore, would seem to be worthy of publication.

The recorded cases are those published by Young (1), Ruge (2), and Hepburn (3) in 1879, 1895, and 1896, respectively. The medial and part of the lateral circumflex arteries of Young's case are described as having arisen from the femoral by means of a common stem of origin; the decending ramus of the lateral circumflex and the only two perforating arteries present arising separately. In Ruge's case the first perforating artery arose from the medial circumflex, the second from the lateral circumflex, while the third arose from the femoral. The two circumflex arteries of Hepburn's case arose from the femoral by means of a common stem of origin. The origins of the first and second perforating arteries were combined in a similar manner, as were also those of the third and fourth perforating arteries.

The arteries of the right thigh of the case that forms the subject of the present communication were distributed in the usual way. The left femoral artery gave origin to three large branches in addition to the a. genu suprema, and the usual small inguinal and muscular branches. The first large branch arose 4.5 cm. below the inguinal ligament and after a course

of 3.5 cm. divided into a medial circumflex artery of the ordinary character, and a branch that gave origin to the first two aa. perforantes. The latter branch passed posteriorly to the adductor longus muscle, and was related to its accompanying vein in the same manner as the normal profunda artery; it gave a small branch to the gracilis. At 9 cm. from its place of origin, it divided into the first and second perforating arteries, both of which pierced the adductor brevis and magnus muscles. The second branch, about the same size as the first, was the lateral circumflex artery, it arose 9.5 cm. from the inguinal ligament. The third branch, about double as large as either of the others, arose 18.7 cm. beyond the inguinal ligament, and was unaccompanied by a vein. After having given origin to two small branches to the adductor magnus, it divided 6 cm. from its origin, into the third and fourth perforating arteries, which pierced the adductor magnus to be distributed to the hamstring muscles.



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- 1 YOUNG, A. H. 1879 Abnormal arrangement of the branches of the femoral artery. Jour. Anat. and Phys., vol. 13.
- 2 RUGE, G. 1895 Varietäten im Gebiete des Arteria femoralis des Menschen. Morph. Jahrb., Bd. 22.
- 3 HEPBURN, D. 1896 Double profunda femoris artery. Jour. Anat. and Phys., vol. 30.

Resumen por el autor, Zeno Payne Metcalf,
North Carolina State College and Experiment Station.

Algunas notas de laboratorio.

En el presente trabajo el autor discute brevemente algunos métodos técnicos de laboratorio. Recomienda el papel bromuro en vez de placas de vidrio para obtener negativas para reconstrucciones en placas de cera, evitándose de este modo el hacer positivas, puesto que las negativas en el papel bromuro sirven para todo propósito. Para placas de cera el autor recomienda el uso de las hojas de cera pura de abejas obtenidas para la manufactura de los panales, principalmente porque es fácil de procurar y es barata. El autor describe y representa un microscopio simplificado para el dibujo, provisto de una lámpara Mazda. Este microscopio presenta sobre otros microscopios similares la ventaja de que con él se obtiene una serie extensa de aumentos con un pequeño número de lentes. También describe el autor una escala duplicadora, que se representa en el trabajo. Esta escala se emplea para para representar el lado complementario de un dibujo bilateral.

Translation by José F. Nonidez
Cornell Medical College, New York

SOME LABORATORY NOTES

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THREE FIGURES

The following notes on laboratory practice are offered for the benefit of other workers. No claims of originality are made, but the writer has frequently noticed that little individual laboratory practices are of use to other workers and frequently have a wider application than is usually appreciated. Neither is it intended to imply that the methods here discussed are the best methods, but if these notes stimulate any one to produce better methods they will have served their purpose.

SOME POINTS ON WAX-PLATE RECONSTRUCTION

Lewis (*Anat. Rec.*, vol. 9, pp. 719-729, 1915) has recently given some very valuable points on reconstruction, but the following points seem worthy of mention. Instead of using glass plates for negatives, it is much easier, more direct, and cheaper to use bromide-paper. The bromide-paper negatives can be used instead of positive prints from the glass negatives, as it really makes no difference in reconstruction whether the photograph we are using is a negative or a positive. Hence all that is necessary is to make the bromide-paper negative and then transfer it to the wax plate. Bromide-paper is handled very much like a glass plate, or the popular gas light papers, such as Velox, Cyko, Artura, etc., but as detailed directions are enclosed with each batch of paper it is not necessary to give them here. Thus we simplify the process greatly and in addition cheapen the process very much, for the large-size plates used are rather expensive. The paper negatives are convenient to store and are not easily injured. Bromide-paper is to be preferred, too,

because it gives flatter, softer negatives than most plates, and because it can be handled in a strong yellow light with ease and comfort. Most types of plate-holders used with photomicrographic cameras are fitted to take either plate or bromide-paper, and if one has such an apparatus no modifications need to be made. If one is provided with a projection microscope only and desires to use the darkened laboratory as a camera, it is very easy to arrange a printing frame with a clear glass plate so that the image can be projected onto it. The printing frame is then used to carry the bromide-paper. A possible objection to the bromide paper is that it requires a somewhat longer exposure than an ordinary plate, but when it is remembered that it is not necessary to make a positive from this negative it will be seen that the process is really very much shortened.

The making of wax plates is a rather tedious, laborious process, but if the plates are purchased from dealers they become very expensive especially if they are to be used by beginners. Hence I was very much interested to know that in the process of manufacturing comb honey and other foundation the beeswax was first smoothed out in a fairly uniform sheet and to know that these sheets could be purchased from foundation manufacturers at a cost very little in advance of the cost of raw beeswax. While these sheets are not absolutely uniform in thickness and while they are not a stated number of millimeters thick, the fact that they can be bought very cheaply compared to the reconstruction wax sheets leads me to believe that they are deserving of recognition, especially by the beginner. Perhaps too much emphasis has been laid upon the fact that wax sheets must be absolutely uniform in thickness. It is well to remember that reconstruction is really drawing in three dimensions and that there may be other errors besides the errors in the thicknesses of the wax plates used. From two manufacturers I have been able to secure three thicknesses of wax called by the manufacturers sheeter wax, brooder sheets, and plain sheets. These were cut into pieces 12 x 12 inches. The sheeter wax averages 2.15 mm. in thickness, the brooder sheets average 1.23 mm. in thickness, the plain sheets average 4 mm. in thickness. It

takes but a very simple calculation to show that if we are reconstructing sections $10\ \mu$ thick and are using a wax plate 2.15 mm. in thickness our magnification must be 100 times 2.15, or $215\times$, if one plate is to be used for each section. If every other section is used, our magnification would be 50 times 2.15, or $107.5\times$, and so for any other combination of thickness of section and thickness of wax plate. The formula is

$$\frac{1000}{\text{thickness of section in } \mu} \times \text{thickness of wax plates} = \text{magnification required.}$$

It is a very small matter to adjust the photomicrographic apparatus for any magnification with the aid of a stage micrometer and a millimeter scale. Thus, if we wish to secure a magnification of 215, a stage micrometer ruled to 0.1 mm. is inserted into the photomicrographic microscope and the lens selected that will give approximately our required magnification; then by moving the ground-glass screen backward and forward we can get a position where the lines of the stage micrometer as projected on the screen are separated by a distance of 21.5 mm., and we have the proper magnification. These odd magnifications are usually as easy to secure as the $50\times$, $100\times$, and $200\times$ that are generally recommended in wax-plate reconstruction.

A DRAWING MICROSCOPE

The drawing projection microscope here described is very simple and easily constructed, and yet it has proved entirely satisfactory and compares very favorably with the much more expensive Edinger drawing apparatus. It has the advantage over the old-style Edinger apparatus of using a mazda lamp instead of an arc. The condenser is the ordinary microscope condenser and the body tube is narrow, hence in these respects it is not as convenient as the Edinger apparatus, but in our work we have found the occasions when we need the double condenser rather rare, and with low-power objectives the condenser may be removed entirely, and by shifting the lamp house fairly satisfactory results can be secured.

This apparatus has combined the following advantages: first, it is vertical; secondly, the lamp and microscope can be readily

adjusted independently of each other; thirdly, it uses a mazda lamp as a light source, thus avoiding the trouble of adjusting carbons; fourthly, the microscope can be brought within 40 cm. of the drawing-board or elevated to a distance of 70 cm. thus giving a great range of magnifications with a limited number of objectives and oculars, as is shown by the following table:

Table of magnification

	DISTANCE MICROSCOPE STAGE TO DRAWING BOARD			
	40 cm.	50 cm.	60 cm.	70 cm.
16 mm. objective front lens removed no eyepiece	9×	12×	15×	18×
16 mm. objective front lens removed 4×	13×	21×	29×	36×
16 mm. objective front lens removed 8×	23×	36×	50×	63×
16 mm. objective no eyepiece	21×	26×	31×	36×
16 mm. objective 4×	38×	58×	78×	98×
16 mm. objective 8×	70×	102×	137×	173×
4 mm. objective 4×	200×	300×	400×	500×
4 mm. objective 8×	350×	510×	680×	850×

In its essential features the apparatus consists of a strong table with an ordinary white-pine drawing-board, for a top. To this table are bolted two square uprights (fig. 1 *u*) 22 x 30 inches, bolted together so as to form a slot which will just pass a quarter-inch thumb or wing-nut bolt. These uprights form the optical bed along which the other parts of the apparatus may be clamped in any position by means of winged nuts (fig. 1, *w*). The lamp house (fig. 1, *h*) consists of a small mazda lantern-slide projector apparatus without the lantern-slide carrier or the projecting lens. This lamp house carries a 400-watt concentrated filament mazda projection bulb backed by a concave mirror which gives a strong steady light. The lamp house is fastened to the optical bed by means of two wing-nuts which pass through a board (fig. 1, *b*) to which the lamp house is securely bolted. The microscope (fig. 1, *m*) is fastened in a similar manner, but it is necessary to have the microscope block (fig. 1, *m b*) much thicker, so that the optical axes of the light and the microscope will center. The microscope is securely fastened to the micro-

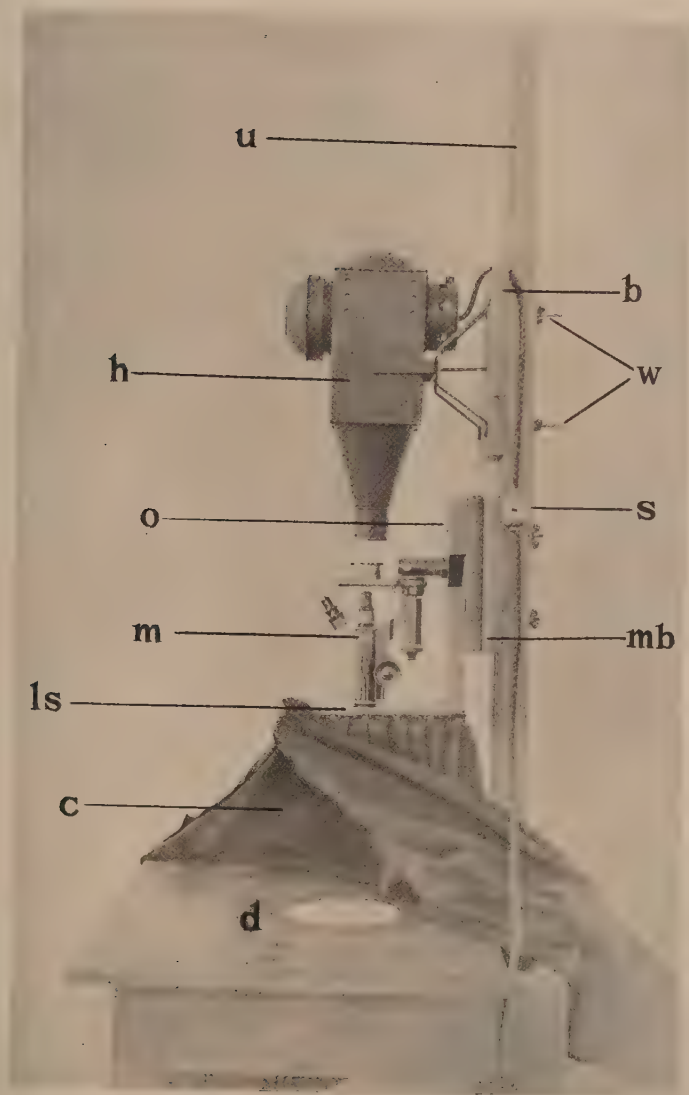


Figure 1

scope block by means of blocks which are slotted to receive the prongs of the horseshoe base of the microscope. The base is held securely by a piece of strap-iron (fig. 1, *o*), which is held in place by means of two screws. We used an old discarded microscope for this purpose, but it would be very simple to fasten the strap-iron by means of wing-nuts, in that case any microscope could be clamped in place for use and then unclamped for laboratory use. The lower part of the microscope block is projected and has a light shield (fig. 1, *l s*) fastened at right angles. This light shield is slotted to receive the tube of the microscope and has a dark curtain (fig. 1, *c*) tacked to its edges, so that the apparatus can be used in a lighted room.

The cost of the apparatus exclusive of the microscope was as follows:

1 lamp house with 400-watt mazda lamp.....	\$32.00
1 table.....	5.00
1 drawing board.....	1.25
Lumber for optical beds, etc.....	.50
1 dozen bolts.....	.10
$\frac{3}{4}$ yard black broadcloth.....	2.25
Total.....	\$41.10

A DUPLICATE SCALE

Having a great many bilaterally symmetrical drawings to make, we had a special scale made as illustrated (fig. 2). This scale is 30 cm. long and reads from the center toward both ends. One edge is graduated in millimeters and has every centimeter numbered. The other edge is graduated in centimeters only. The scale is used in the following manner: A central line is drawn along the central axis of the drawing and one-half of the drawing outlined by means of the camera lucida or by any other method. The scale is then laid on the drawing with its center on the central axis of the drawing. It is a very simple matter to move the scale along the axis and to read the location of critical points on the outline which has been drawn and to plot them on the other end of the scale.

A simple illustration, such as the outline of the beetle here presented, will make the matter clear. *A B* is the central axis

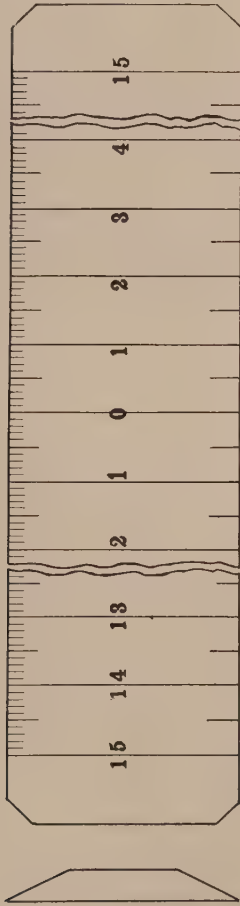


Figure 2

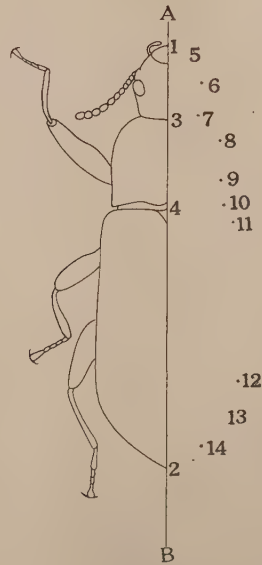


Figure 3

of the drawing and the left side of the outline has been secured. The problem is to secure the outline of the right side. The scale is centered on the axis *A B* and moved along until the

base of the clypeus is reached. It is noted that this point is 8 mm. from the central axis, and a point (fig. 3, *point 5*) on the right-hand side of the axis is located, the same number of millimeters from the central axis. In the same way the scale is moved along and other critical points are located (fig. 3, *points 6 to 14*). The number of points necessary will depend upon the complexity of the outline and will be in inverse ratio to the skill of the draughtsman. I have found this a very useful scale and far superior to transferring by carbon paper or other methods that I have tried, especially when working on wash or water-color drawings where the number of marks on the paper should be reduced to the minimum.

ON THE PATENCY OF THE FORAMEN OVALE IN FILIPINO NEWBORN CHILDREN

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THREE FIGURES

The scarcity of reports on the patency of the foramen ovale in the anatomical literature, specially from this country, and the desire of perhaps throwing some light on the etiology of the abnormally high rate of infant mortality in these islands have induced us to make some observations on the hearts of newborn babies coming to our morgue from the different hospitals and out-patient clinics of Manila.

The present work is offered only as a preliminary note, and as such it is incomplete and based on a small number of cases. It is intended to have it followed later by more extensive observations.

MATERIAL AND TECHNIQUE

Our series includes 134 cases, 80 males and 54 females, the majority of which were stillborn and outwardly at least apparently normal and full-term fetuses (117 stillbirths, fourteen under twelve hours and three under six days).

We are only considering the morphology, position, and different degrees of patency of the foramen ovale, but in order to establish the stage of development of the fetus and of its heart we have taken in addition the measurements of body length, body weight, size of the heart and of its different orifices, cardiac weight, and the thickness of cardiac walls.

After determining the body weight and the body length in each case, the heart was removed by cutting the great vessels uniformly at the level of the superior atrial borders. It was then weighed fresh with the contained blood unremoved and with calipers, the greatest vertical, transverse, and antero-

posterior diameters were determined. The difficulties in keeping the parts in situ while measuring and the consequent distortions following the opening of the cardiac cavities have decided us to fix the organ in formalin (10 per cent) before undertaking any internal examinations. About a month later, the heart was again weighed, its greatest diameters once more taken and in addition the greatest circumference of its base was determined.

The heart was now opened by four different incisions:

1. A vertical incision was made along its dorsal wall extending from the superior caval orifice down to the inferior, thence downward to the apex of the right ventricle, cutting through the right atrioventricular orifice. We expose by this incision the right side of the interatrial septum and the right atrioventricular orifice.

2. A second incision was cut along the ventral wall of the right ventricle from the lower end of the preceding, and extending upward to the pulmonary orifice in a direction parallel to the interventricular septum. We expose for examination the pulmonary orifice.

3. A third incision extending from the upper left pulmonary vein along the posterior wall of the heart downward to the bottom of the left ventricle, passing through the mitral opening. We lay open by this cut the left side of the interatrial septum.

4. A fourth and last incision was then made from the cut end of the aorta along the posterior wall of the vessel, the medial wall of the left artium and down to the cavity of the left ventricle, passing through right anterior flap of the mitral valve. We expose here the aortic and mitral orifices.

We measured the thickness of the cardiac walls and the cardiac diameters with calipers, the cardiac circumference with a graduated tape, and the areas of the foramen ovale and of its patent opening with a graduated slide specially devised for the purpose.

We etched on a glass slide an area of 1 sq. cm. which was divided into 100 sq. mm. Below the large square a linear scale divided in tenths of millimeters was etched. This slide was placed as near as possible to the surface to be measured and as nearly parallel to its plane; the number of squares included within the field were counted, partial squares being compensatingly considered, i.e., two halves equal to one, etc.

GENERAL BODY AND CARDIAC MEASUREMENTS

We note from Benestad and Meyer the following figures for the average body weights, body lengths, and cardiac weights of newly born children, to which we have added our own findings:

TABLE I
Different measurements of body lengths, body weights, and cardiac weights

AUTHOR	PLACE	NUMBER OF CASES	MALE	FEMALE	BOTH SEXES
<i>a. Average body weights</i>					
			<i>grams</i>	<i>grams</i>	<i>grams</i>
Issmer.....	Dresden	7612	3320	3214	3267
Wernick.....	Munich	6000	3337	3209	3273
Ingerslev.....	Copenhagen	3450	3381	3280	3330
Kerzmarszky.....	Jena	1700	3484	3344	3414
Paterson.....	Upsala	1675	3595	3455	3525
Wagner.....	Konigsberg	1500	3479	3339	3409
Wolff.....	Basel	1448	3220	3140	3180
C. Martin.....	Berlin	1000	3328	3221	3274
Fuhrmann.....	Petrograd	1000	3490	3185	3337
Bonestad.....	Copenhagen	1979	3528	3410	3469
Meyer.....	United States	1026	3387	3242	3436 ¹
Meyer.....	United States	1027			3185 ²
Katzen.....	Toulouse	1000	3305	3175	3240
Biedert.....			3500	3250	3375
Nañagas.....	Manila	134	2253.7	2251.7	2252.7 ³
<i>b. Average body lengths</i>					
			<i>cm.</i>	<i>cm.</i>	<i>cm.</i>
Katsen.....	Toulouse	1000	49.9	48.9	49.4
Meyer.....	United States	1026	49.6	48.7	49.8
Meyer.....	United States	1027 ¹			48.5
Biedert.....					50.0
Nañagas.....	Manila	134	44.2	44.0	44.1
<i>c. Average cardiac weights</i>					
			<i>grams</i>	<i>grams</i>	<i>grams</i>
Muller.....			16.2	14.4	
Vierordt.....			17.2	15.2	
Nañagas.....			15.5	15.3	
Bovaire and Nicoll.....					21.0
Notori.....					14.5
Nañagas.....					15.4

¹ Negroes. ² White. ³ Stillborn.

Our own general maximum, minimum and average measurements were as follow:

TABLE 2
Body weights, body lengths, and cardiac weights¹

SEX	BODY WEIGHTS			BODY LENGTHS			CARDIAC WEIGHTS		
	Maxi- mum	Mini- mum	Aver- age	Maxi- mum	Mini- mum	Aver- age	Maxi- mum	Mini- mum	Aver- age
Males.....	4630	815	2253	57.0	21.0	44.2	26.0	6.9	15.5
Females.....	3844	850	2251	58.0	21.0	44.0	24.1	6.0	15.3
Average, regard- less of sex.....	4237	832	2252	57.5	21.0	44.1	25.0	6.4	15.4

¹ Weights in grams and lengths in centimeters.

The cardiac weights were averaged from the results in fresh and fixed hearts. For the purpose of establishing the relations between body weights, body lengths, and cardiac weights, we prepared table 3, where the cases were grouped in series varying in weights of 200 grams increase, the measurements representing the averages for the number of cases included in each series.

For a comparative study, we also reproduce here from Scammon the measurements of weights of the heart in the newborn.

Table 33 of Scammon's collection of foetal measurements

BODY WEIGHT	HEART WEIGHT
<i>kgm.</i>	<i>grams</i>
2.0 to 2.5	17.8
2.5 to 3.0	19.5
3.0 to 3.5	21.7
3.5 to 4.0	25.3
4.0 to 5.0	28.6

From table 3 we note that the average cardiac weights bear definite relations with the average body weights, such relations with one or two exceptions consisting in a steady proportionate increase of about 1.13 grams for each 200 grams of increase in body weight. Comparing our results with those given in Scam-

mon's table, it will be noted that the Filipino hearts were correspondingly lighter, the difference varying from 1.42 to 2.50 grams.

Our measurements of the dimensions of the heart are shown in table 4, in which the cases were segregated in groups of increasing cardiac weights.

TABLE 3
Relations between body weight, body length, and cardiac weight

NUMBER OF CASES	BODY WEIGHTS	AVERAGE OF BODY LENGTH	HEART WEIGHTS		
			Minimum	Maximum	Average
	<i>grams</i>	<i>cm.</i>	<i>grams</i>	<i>grams</i>	<i>grams</i>
7	Under 1000	36.0	5.2	12.5	6.67
7	1000-1200	40.0	7.7	15.3	10.00
9	1200-1400	38.5	6.8	21.0	8.84
13	1400-1600	41.5	7.7	12.0	9.60
13	1600-1800	42.3	9.0	15.5	11.11
9	1800-2000	44.0	10.1	15.0	11.92
7	2000-2200	42.5	7.1	19.6	14.30
13	2200-2400	47.1	10.3	24.0	15.68
11	2400-2600	46.3	11.2	24.0	15.83
11	2600-2800	48.0	7.2	26.0	16.42
12	2800-3000	47.6	15.0	21.0	16.93
6	3000-3200	50.2	16.0	20.4	18.60
7	3200-3400	50.4	18.3	25.0	20.90
7	3400-3600	52.2	14.4	41.0	21.27
2	Over 3600	53.0	18.7	19.9	19.30

Our general averages of the above cardiac dimensions were:

	<i>mm.</i>
Greatest circumference.....	92.1
Greatest vertical diameter.....	46.2
Greatest transverse diameter.....	34.9
Greatest anteroposterior diameter.....	22.4

Unfortunately, we find no record of measurements of the heart in the newborn. Barthes and Rillet, quoted by von Stark, give some measurements in children of fifteen months to fourteen and one-half years. Their cardiac circumference varied from 130 to 190 mm. and the vertical diameter from 55 to 90 mm.

From table 4 we find that hearts weighing from 5 to 20 grams showed a consistent increase in all dimensions, which became

TABLE 4
Cardiac dimensions in relation to cardiac weights

HEART WEIGHT	NUMBER OF CASES	CIRCUMFERENCE	DIAMETERS		
			Vertical	Transverse	Anteroposterior
<i>grams</i>					
5-10	29	72.6	35.7	27.5	18.2
10-15	46	86.3	42.9	31.9	21.0
15-20	32	97.1	45.7	36.5	22.8
20-25	13	100.0	48.9	37.8	26.1
25-30	5	104.5	58.0	41.2	24.0

less marked in the heavier hearts. This apparent discrepancy between the increase in weight and the lessened increase in dimensions is probably to be accounted for by a greater increase in the thickness of cardiac walls.

With reference to the parietal thickness of the heart, we found the following:

TABLE 5
Comparative measurements of thickness of the ventricular walls

AUTHOR	AGE	THICKNESS OF VENTRICULAR WALLS	
		Right	Left
		<i>mm.</i>	<i>mm.</i>
Gibson and Gillespie.....	Full-term (s.b.)	4.0	3
Gibson and Gillespie.....	Full-term (lived 24 hrs.)	3.0	4
Notori.....	(Newborn)	4.0	4
Nañagas.....	(Stillborn)	3.6	4

Our average measurements of the circumference of the other cardiac orifices were:

	<i>mm.</i>
Right atrioventricular orifice.....	27.5
Left atrioventricular orifice.....	25.2
Pulmonary orifice.....	15.9
Aortic orifice.....	13.6

Table 6 shows the measurements of the cardiac orifices and cardiac walls in relation to cardiac weights.

The left atrioventricular, the aortic, and the pulmonary orifices showed a steady and proportionate increase in size with the increase cardiac weights, the right atrioventricular opening, however, appeared to remain stationary in hearts weighing 20 grams or more.

The thickness of the two ventricular walls increased about the same at the rate of 5 mm. for every 5 grams of excess in cardiac weight. The wall of the left ventricle was thicker than the right throughout the series, the difference being greater in lighter hearts.

TABLE 6

Measurements of cardiac walls, cardiac orifices and cardiac weights

HEART WEIGHTS	NUMBER OF CASES	THICKNESS OF VENTRICLE		CIRCUMFERENCE OF CARDIAC ORIFICE			
		Right ventricle	Left ventricle	Right atrio-ventricular orifice	Left atrio-ventricular orifice	Pulmonary orifice	Aortic orifice
<i>grams</i>		<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>
5-10	30	26.0	32.0	23.5	21.5	12.8	11.5
10-15	47	35.0	37.0	27.0	24.5	15.0	13.0
15-20	31	39.9	43.5	30.0	26.5	17.0	14.5
20-25	12	45.0	48.0	29.5	28.5	19.0	15.5

Revising the above data, we find that the average body weight and body length in our series were less than those given by other observers. In our mind this fact, however, cannot be construed as spelling lack of development and immaturity of our foetuses. The probabilities are that the measurements of the other authors were taken on the living in some obstetrical clinics, while ours were made on dead subjects and only after forty-eight hours of steady refrigeration. Moreover, it is a well-known fact that Filipinos are a small race and, as noted elsewhere, the foetuses were outwardly normal in appearance.

The cardiac weights though correspondingly smaller, as compared to those given by Scammon, yet our general average appears almost normal when compared with those of Muller, Vierordt, Notori, and others. We are unfortunate in not finding records of measurements of cardiac dimensions in the literature,

yet if we compare our average figures with those of Barthes and Rillet for babies fifteen months old, the discrepancy appears to be only what might be expected.

The measurements of the thickness of the ventricular walls were almost identical with the findings of Gibson and Gillespie and Notori, though in our series the left ventricle showed a trifle excess in thickness as compared to the right.

We may safely conclude, therefore, that our foetuses as well as their hearts were not far from their normal development.

TABLE 7
Frequency of the three types of foramen ovale

SEX	TOTAL NUMBER OF CASES	CIRCULARS		OVALS		TRIANGULARS	
		Cases	Percent- age	Cases	Percent- age	Cases	Percent- age
Male.....	63	28	44.4	22	34.9	13	20.7
Female.....	44	27	61.3	9	20.4	8	19.3
Total.....	107	55	53.4	31	27.6	21	20.0

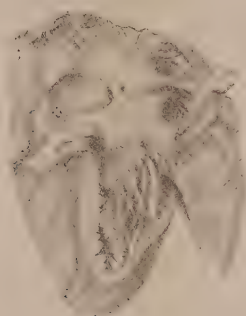
FORAMEN OVALE

The foramen ovale was studied in 107 cases. It showed considerable variation in shape, however; we could distinguish three principal types distributed as follows (table 7 and figs. 1, 2, and 3).

a. Circular foramen, present in 55 cases (28 males and 27 females), or in 53.4 per cent of the series. It is more frequently encountered in females. The posterior border was the least prominent, the other margins of the foramen merging gradually with the posterior atrial wall at this point.

b. Ovale type, found in 31 cases (22 males and 9 females), or in 27.6 per cent. The long axis of the foramen was directed anteroposteriorly and the superior and inferior margins were much more prominent than the edges in front and behind. This type was found more in males.

c. Triangular form, present in 21 cases (13 males and 8 females), or in 20 per cent, and with equal frequency in both



sexes. The foramen had one of its angles directed anteriorly and the two posteriorly. The sides of the anterior angle were better developed than those of the posterior angles.

TABLE 8
Areas of foramen ovale (in sq. mm.)

CIRCULARS				OVALS				TRIANGULARS			
Males		Females		Males		Females		Males		Females	
Cases	Area	Cases	Area	Cases	Area	Cases	Area	Cases	Area	Cases	Area
1	6	1	5	1	10	1	17	1	12	1	13
1	12	1	9	1	13	1	19	2	14	1	14
1	13	1	11	2	16	1	20	1	15	1	18
1	14	1	12	1	19	1	22	1	17	1	24
1	16	2	13	1	23	1	25	1	19	1	26
2	17	1	14	1	25	1	28	1	24	1	37
1	19	2	16	1	27	1	32	1	25	1	39
2	20	3	17	2	28	1	44	1	26	1	95
1	21	1	19	1	29	1	45	1	27		
1	22	2	20	1	33			1	28		
1	23	1	21	2	36			1	36		
1	24	3	23	1	38			1	54		
2	26	1	24	1	39						
2	27	1	26	1	4						
1	29	1	28	3	43						
2	31	2	30	1	52						
2	34	1	37	1	85						
1	36	1	46								
1	39	1	56								
1	41										
1	42										
1	50										
28	25.6	27	21.77	22	35.18	9	18	13	23.9	8	33.2

The foramen ovale was uniformly found located in the posterior two-thirds of the interatrial septum, sometimes at its middle (in 66 cases, or 61.4 per cent), others higher up near the superior caval opening (in 39 cases, or 36.4 per cent), and in 13 cases (or 12 per cent) in its lower section near the valve of Thebesius. The areas of the foramen are given in table 8.

The general average in the total series was 26.69 sq. mm. From the above table it will be seen that the circular type showed the smallest area, averaging only 23.69 sq. mm.; the oval form came next, with a general average of 26.59 sq. mm., and the triangular shaped foramina appeared largest, with an average of 28.55 sq. mm. Both the circular and oval types showed larger average areas in males than in females, while in the triangular forms the conditions were reversed. In general we found that most of the cases varied in area between 20 and 30 sq. mm.

TABLE 9
Areas of patency of foramen ovale (sq. mm.)

CIRCULAR				OVAL				TRIANGULAR			
Males		Females		Males		Females		Males		Females	
Cases	Area	Cases	Area	Cases	Area	Cases	Area	Cases	Area	Cases	Area
2	3.0	1	1.5	3	2.0	3	2.0	1	1.0	2	3
1	4.0	5	2.0	2	2.5	1	3.0	1	1.5	1	18.0
2	5.0	1	2.5	1	3.0	1	4.0	3	3.0		
1	6.0	2	3.0	2	3.0	1	5.0	2	4.0		
5	7.0	1	4.0	4	4.0	1	6.0	1	6.0		
1	8.0	1	5.0	1	5.0						
1	26.0			2	6.0						
				1	27.0						
13	7.33	11	2.09	16	5.0	7	3.42	8	3.18	3	38.0

PATENCY OF THE FORAMEN OVALE

Addison found in his series 33.3 per cent of patent cases. We encountered a much greater number of cases in ours. Out of 107 cases examined, 58 showed patency, or 54.2 per cent; 36 of these were met among males (57.1 per cent) and 22 cases were found in females (64.7 per cent).

The above cases were distributed in the different types of foramen ovale as shown in table 9.

We found patency in 24 out of 55 circular cases (42.7 per cent); in 23 out of 31 oval cases (74.1 per cent), and in 11 out of 21 triangular cases (52.3 per cent). The area of the aperture

varied from 1 to 27 sq. mm., the largest being found in males of the oval and circular types. Most of our cases varied in area from 2 to 5 sq. mm.

The position of the aperture of patency appears to vary with the position of the septa of the foramen, so that the opening is pushed upward when the septum primum has its free edge directed also superiorly and vice versa when the conditions are reversed. The edge of the septum secundum apparently has a contrary effect in directing the location of the opening, i.e., if the free edge of the septum primum is directed upward it pushes ahead the aperture, while the edge of the septum secundum meeting it from above tends to shift ahead of it the opening, and between the two of them they reduce its area of extent. In over one-half of the cases the opening appeared above the middle horizontal plane bisecting the foramen ovale. This is only to be expected from the most common position of the two septa: the septum primum, postero-inferiorly and the septum secundum, anterosuperiorly. This same position of the septa accounts for the oval shape of the aperture and the oblique direction of its long axis from above and behind forward and inferiorly. Physiologically, this orientation of the opening appears favorable in directing the blood stream from the inferior caval orifice to the left atrium.

In 78 cases the septum primum was posterior in position, while the septum secundum was anterior; in 42 cases the septum primum was postero-inferior, while the septum secundum was anterosuperior in 34 cases, and finally the septum primum was posterosuperior in one case, and the septum secundum antero-inferior in 8 instances.

Reviewing the tables giving the sizes of the heart, and the areas of the foramen ovale and its aperture of patency, we failed to find any definite relation between the size of the heart and that of the foramen, or between the area of the foramen ovale and its orifice of patency.

SUMMARY

Summarizing our findings:

1. Filipino fetuses in general are smaller and lighter than European or American fetuses.

2. The general average weights of foetal hearts in our series was about the same as those reported by other observers. Cardiac weights increased proportionately with body weight, this increase was, however, smaller than given in Scammon's table 33.

3. Cardiac dimensions showed a definite and proportionate increase with the increase in cardiac weights; this increase, however, was less marked in hearts heavier than 20 grams, probably because of greater thickening of cardiac walls.

4. The thickness of the two ventricular walls in our cases, was about the same as reported by other workers, but in our series the left ventricle was uniformly the thicker.

5. The thickness of both ventricles definitely and proportionately increased with the cardiac weights.

6. The right atrioventricular orifice showed the largest circumference; the aortic, the smallest. The left atrioventricular, the aortic, and the pulmonary openings steadily increased in size with the weights of the hearts, but the right atrioventricular orifice remained almost stationary in hearts heavier than 20 grams.

7. Filipino fetuses and foetal hearts of this series were probably normal in development.

8. The foramen ovale was present in three different shapes: circular, oval, and triangular; the first of which was the smallest and most frequently encountered, and the last type the largest and least common.

9. The circular and oval types of foramen ovale were larger in males than in females, while in the triangular form the conditions were reversed. The circular type was more commonly encountered in females, while the other two types were more frequent in males.

10. In location the foramen ovale was most commonly found in the middle section of the posterior two-thirds of the interatrial septum.

11. Our percentage of patency of the foramen ovale was greater than reported by Addison. More cases of patency were met in females.

12. The area of the opening of patency was largest in males. It varied from 1 to 27 sq. mm., the majority of cases were 2 to 5 sq. mm.

13. In position the opening was more commonly found above the middle horizontal plane of the foramen ovale.

14. No definite relation could be observed between the sizes of the hearts and of the foramen ovale, nor between the size of the foramen ovale and the aperture of patency.

We feel that we are not in possession of sufficient data to offer conclusions explanatory of the high frequency of occurrence of patent foramen ovale in Filipinos; we believe, however, that this fact should be taken into account when considering the various and different etiological factors of our excessive infant mortality.

Our thanks are due to Dr. Arturo Garcia for helpful suggestions in the present work.

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Resumen por G. Carl Huber, por el autor Sabas E. Yap.

El músculo esternal de los filipinos.

En 136 cadáveres adultos disecados, el autor ha observado la presencia de un músculo esternal en cinco casos, en cuatro monstros anencefálicos entre diez examinados, y en dos fetos entre diez fetos normales estudiados. Los casos observados se describen detenidamente, ilustrando las descripciones con figuras. Las variaciones relativas al origen é inserción, relaciones, y la inervación, encontrados en los casos descritos y en otros publicados en la literatura han sido reunidos en una serie de cuadros. El autor presta particular atención a la homología del músculo esternal, encontrando diversas opiniones en la literatura, las cuales discute críticamente, llegando a la conclusión de que este músculo pertenece al grupo de los músculos pectorales—una opinión primeramente expresada por Bardeleben y apoyada más tarde por Cunningham y Shepherd por el hecho de que el músculo esternal está a menudo inervado por los nervios torácicos esternales.

Translation by José F. Nonidez
Cornell Medical College, New York

MUSCULUS STERNALIS IN FILIPINOS¹

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TWO PLATES (TEN FIGURES)

The musculus sternalis is a small muscle of the thorax encountered in the dissection-room in no less than 3 per cent of all cases. For a long time it has aroused the interest of many anatomists because of the different possibilities of explaining its homologies. It was described for the first time in 1604 by Cabrolus (1), but its connections and relations were not precisely understood until 1723, when Du Puy gave a clear account of the muscle. From that time on this muscle has been very extensively discussed, and in recent years its homology has taxed the ingenuity of many investigators, and various interesting hypotheses had been formulated in their attempts to explain it. Its varied nerve supply, connections, and relations which have been considered as important points in deciding its homology make of this muscle an interesting specimen to anatomists.

It has been found in both sexes in adult cadavers and in a surprisingly large proportion in anencephalous fetuses. It has been reported in different races. Its occurrence in Filipinos is the subject of this short paper.

The present work comprises an observation on 136 cadavers dissected in the Department of Anatomy for the last five years, and includes besides a special dissection made on ten anencephalous monsters (four males and six females) and ten apparently normal fetuses (five males and five females).

I was able to collect data of its presence in five out of the 136 adult cadavers, or a proportion of about 3.6 per cent, and found it present in four anencephalous monsters of the ten examined (40 per cent) and in two of the normal fetuses (20 per cent).

¹ Read before the Manila Medical Society, October 4, 1920.

Two of the five adult cadavers showing the muscle were males, and in each one it was present on only one side; the remaining three were females, and in each the muscle was bilateral. We also found the muscle bilateral in the four monsters which were all females and in one male and one female normal fetus. We therefore had a total of twenty specimens. Attention is invited to the fact that most of our dissected adult cadavers were males.

The following are the cases observed:

Case I. Male, 36 years old, prisoner. Musculus sternalis, unilateral, left side. It measured 2 cm. at its widest part and about 10 cm. in length. It originated by a flattened tendinous band from the pars abdominalis of the left pectoralis major at the level of the sixth rib about 3.75 cm. from the center of the xiphoid process of the sternum.

Its fibers ran upward and medially and gained attachment by a small tendon to the second costal cartilage, blending there with the sternal origins of the pectoralis major and the sternocleido mastoids from the manubrium sterni. The nerve supply was furnished by fibers from the medial anterior thoracic which penetrated the deep surface of the muscle near its medial margin.

Case II. Female, 85 years of age, musculus sternalis, bilateral. Both muscles were about the same in length and width, 10 cm. long and 2.5 cm. wide. Each originated from the pectoralis major at the level of the fourth rib, the fibers ran upward and medially and were inserted to the anterior surface of the sternoclavicular joint, blending with the sternal origin of the corresponding sternocleido mastoid muscle. The nerve supply was also from the anterior thoracic nerves.

Case III. Female, insane, 89-years old, musculus sternalis, bilateral. The left muscle was shorter and much smaller than the right. It originated by a tendinous band from the left rectus sheath and the sixth rib, the fibers ran upward and medially to be inserted by tendinous band into the manubrium sterni at the level of the second rib. A tendinous slip separated from this tendon of insertion and crossed medially to unite with the tendon of the right musculus sternalis. The nerve supply was from the anterior thoracic.

The right muscle originated also from the right rectus sheath and sixth rib by a tendinous band, and ran upward and medially to gain insertion in common with the sternal origins of the two sternocleido mastoid muscles. The nerve supply was identical to that of the left muscle.

Case IV. Female, insane, 78 years old, musculus sternalis, bilateral. Both muscles were of about the same size (fleshy portions about 4 cm. long and 1.5 mm. wide) each originating by a long tendinous slip from the fifth costal cartilage and by radiating muscular fibers from the aponeuroses of the external oblique muscle of the abdomen. The course of the muscle fibers was similar to that of the others, upward and medially

and were inserted to the junction of the manubrium and the body of the sternum. The nerve supply was not determined. (We were not able to make a drawing of this case.)

Case V. Male, prisoner, 20 years old, musculus sternalis, unilateral, right. It measured 10 cm. long and 2.5 cm. wide. It originated from the fascia covering the lower portion of the right pectoralis major, it ran upward and medially and was inserted by two tendinous slips, the upper one to the middle of the lower part of the manubrium sterni at the level of the second rib, and the lower slip to the middle of the body of the sternum at the level of the third rib. The nerve supply was from one of the intercostals.

Case VI. Female normal foetus. Musculus sternalis, bilateral. The right muscle was 4.4 cm. long and 0.8 cm. wide (widest part). It originated by muscular fibers from the sixth cartilage and the costal origin of the pectoralis major. The fibers coursed upward and medially gradually tapering to a slender muscular band which was continuous with the right sternomastoid. The nerve supply was a twig from the lateral anterior thoracic. The medial border of the origin was about 0.6 cm. from the midsternal line.

The left was 4 cm. long and 0.95 cm. wide (widest part). Origin by a wide and flat tendinous band from the aponeurosis of the external oblique, the rectus sheath, and costal portion of the pectoralis major. It ran upward and medially and was partly inserted by muscular fibers to the sternal portion of the pectoralis major at the level of the second interspace and partly by muscular fibers which crossed the middle line of the sternum at the level of the second rib to be inserted into the right pectoral major. The nerve supply not identified. The medial border of the origin was 1.1 cm. from the midsternal line.

Case VII. Male normal foetus. Musculus sternalis bilateral. The right muscle was 3.4 cm. long by 0.5 cm. wide at widest point. Origin, by aponeurotic band from the costal portion of the pectoralis major at the level of the fifth interspace, the fibers course upward and medially and at the level of the third interspace, the muscle bifurcated, the lateral muscular fasciculus was inserted to the sternal portion of the great pectoral at the level of the third rib, and the medial band which was semitendinous was continuous with the sternomastoids above. The nerve supply was not found. The medial border of the origin was 0.9 cm. from the midsternal line.

The left was 3.7 cm. long and 0.9 cm. wide (widest part). It originated by muscular fibers from the sixth rib and the adjoining costal portion of the great pectoral, the fibers course upward and medially, tapering to a semitendinous band which also become continuous with both sternomastoids. The nerve to the muscle was not found. The medial border of the origin was 0.95 cm. from the middle line.

Case VIII. Anencephalous foetus, female. Musculus sternalis, bilateral. The right muscle was much larger than the left, it measured 4.5 cm. long and 1.7 cm. wide. It originated by a tendinous band partly from the aponeurosis of the external oblique and partly from the

pars abdominalis of the right pectoralis major. The medial border of its origin was 1.2 cm. from the middle line. The fleshy fibers ran upward and medially, making a curve convex outward and gradually tapering to be inserted by muscular fibers to the middle of the lower portion of the manubrium sterni and by deep fibers to the second costal cartilage. There was a distinct triangular interval between this muscle and the clavicular and abdominal portions of the pectoralis major, where its nerve was seen coursing to penetrate the substance of its deep surface. By reflecting laterally the upper portion of the clavicular and sternal portions of the pectoralis major, this nerve was traced over the pectoralis minor from the musculus sternalis upward and laterally to the point where it pierced the costocoracoid membrane, where it was identified as the medial anterior thoracic nerve.

The left muscle originated by a flat thin tendon not unlike ordinary fascia from the lower part of the costal portion of the left pectoralis major, it ran upward and medially, and at the level of the second rib, it was joined at its lateral side by a small muscular slip from the left pectoralis major. It divided at this level into two flat tendons, the lateral one was inserted with the right muscle to the middle of the lower portion of the manubrium sterni and the medial tendon to the middle of the upper portion of the body of the sternum. This muscle measured 2.7 cm. long and 0.4 cm. wide. The medial border of its origin was 0.5 cm. from the middle line. No nerve to this muscle was observed.

Case IX. Anencephalous fetus, female. Musculus sternalis, bilateral. The right muscle was smaller than the left. It measured 2 cm. long and 0.7 cm. wide. Its origin was by muscular fibers from the pars abdominalis of the right pectoralis major, some of the fibers originating from its deep surface. The muscle ran upward and medially and was inserted by fascial attachment to the sternal portion of the right pectoralis major at the level of the third rib. The medial border of its origin was 1.2 cm. from the middle line. Its nerve supply pierced both pectoral muscles and reached the musculus sternalis at its deep surface. It was identified to be the medial anterior thoracic.

The left muscle was much larger, it measured 3.5 cm. long and 1.1 cm. wide. Its origin was by a flat tendinous band from the aponeurosis of the external oblique, it ran upward and medially and was inserted by two tendinous ends, the lateral to the third costal cartilage and the medial crossed the median line to the right side and was inserted in common with that of the right muscle to the middle sternal portion of the right pectoralis major at the level of the third rib. The medial border of its origin was about 1.4 cm. from the middle line. Its nerve supply was identical with that of the right muscle.

Case X. Anencephalous monster, female. Musculus sternalis, bilateral. The right muscle was much larger than the left measuring 5.4 cm. long and 1.7 cm. at its widest part. The medial border of the origin was 1.8 cm. from the midsternal line. It originated from rectus sheath and aponeurosis of the external oblique, the fibers ran upward and medially, and at the level of the third costal cartilage it bifurcated, the lateral

muscular band was inserted into the sternal portion of the pectoralis major at the second interspace and the medial end tapered in a tendinous band inserted into the sternal portions of the two pectorals at about the median line. The nerve supply was by a filament from the third intercostal.

The left was very small, it measured 2.1 cm. long and 0.3 cm. at widest portion. Its origin was muscular from the costal portion of the great pectoral at the level of the fifth rib 1.1 cm. from the median line of the sternum, the fibers ran upward and medially and were inserted directly to the sternal portion of the pectoral at the level of the upper border of the third rib. Nerve supply was not found.

The right muscle was larger. It measured 4.4 cm. long and 1 cm. wide. It was apparently made up of two parts, separated by denser fascia, one superficial and lower originated from the aponeurosis of the external oblique and the abdominal portion of the great pectoral, its fibers ran upward and medially, and at the level of the fourth costal cartilage they blended with those of the deeper part and continued upward to gain insertion by semitendinous connection to the manubrium sterni. The deeper portion originated by muscular slips from the aponeurosis of the external oblique and by tendinous origin from the costal portion of the great pectoral under cover of the superficial part, and after pursuing a vertically upward course was inserted by muscular attachment to the anterior part of the sternoclavicular joint. The medial border of the origin of the muscle was 1.2 cm. from the median line. Its nerve was not found.

The left was much smaller. It measured 2.2 cm. long and 0.25 cm. wide. Origin, by long slender tendinous slip from the sternal portion of the pectoralis major at the level of the fourth costal cartilage, the fibers ran upward and medially and were inserted directly to the upper border of the manubrium sterni near the median line. Nerve supply not found. The medial border of the origin was 0.4 cm. from the midsternal line.

Table 1 shows the distribution of the muscle.

From the above cases we see that the attachments, relations, and sizes of the musculus sternalis are so manifold that a description of one specimen is not an adequate account for all, no two specimens being exactly alike. In this respect it is different from other muscles of the body, which, as a rule, have a constant origin, insertion, relations, and nerve supply. Its size in our cases varied from 2 cm. to 10 cm. long and from 0.25 cm. to 2.5 cm. wide. We can say, however, that in every case, the muscle was found lying over the pectoralis major at varying distances from the sternum. With regard to origin we found that the muscle

started sometimes from the aponeurosis of the external oblique, at others from the abdominal portion of the great pectoral, rectus sheath, or from the lower costal cartilages. Again this origin varied from fascial bands to muscular or tendinous slips.

Its insertions again were varied. In some cases it was found inserted in the manubrium sterni, in others in the body of the

TABLE 1

SCHOOL YEAR	NUM- BER OF SPECI- MENS EXAM- INED	PRESENCE OF MUSCULUS STERNALIS						INNERVATION
		Cases	Male	Female	Unilateral or bilateral	Num- ber of speci- mens	Per- centage	
<i>a. Musculus sternalis in adult Filipino cadavers</i>								
1915-16	60	I	1		Unilateral	1	1.66	Medial anterior thoracic
1917-18	38	II and III		2	Bilateral	4	5.26	Both anterior thoracic
1918-19	14	IV		1	Bilateral	2	7.14	Undertermined
1920-21	24	V	1		Unilateral	1	4.16	Intercostal
Total	136	5	2	3		8	3.67	
<i>b. Musculus sternalis in Filipino fetuses</i>								
1920	10	VI and VII	1	1	Bilateral	4	20	Lateral anterior thoracic
<i>c. Musculus sternalis in anencephalic Filipino fetuses</i>								
1920	10	VIII to XI		4	Bilateral	8	40	Medial anterior thoracic and third inter- costal

sternum and upper costal cartilages, or even blending with the upper origins of the pectoralis major or the sternal origins of the sternocleido mastoids. Here also the insertion was accomplished either by muscular fasciculi or by one or more tendinous connections. The nerve supply is by no means the same in every case. In our cases, however, two nerves appeared to be the main sources of nerve supply, viz., the anterior thoracics and the intercostals. This finding is confirmed by those of others, as noted in table 2.

The importance of the nerve supply in considering the homology of this muscle was not apparently realized by the older writers, and it is only since Cunningham (2) called attention to this fact that more careful study has been made of this part of the subject.

TABLE 2

Nerve supply of the musculus sternalis (modified after Cunningham)

AUTHORS	NUMBER OF MUSCLES SUPPLIED BY ANTERIOR THORACICS	NUMBER OF MUSCLES SUPPLIED BY INTERCOSTALS
Shepherd.....	7	
Wallace.....	1	
Lamont.....	6	
Dwight.....	2	2
Cunningham.....	17	
Hallett.....		1
Bardeleben.....		2
Yap.....	9	2
Total.....	42	7

TABLE 3

Musculus sternalis in different nationalities (modified after Ruge)

AUTHORS	NATIONALITIES	PERCENTAGE
Chudzinski, Le Double and Testut.....	Negro	8.4
Macalister.....	Irish	6.0
Cunningham.....	Irish	4.4
Gruber.....	Russian	5.26
Le Double.....	French	4.65
Wood.....	English	4.0
Turner.....	Scotts	3.23
Schwalbe and Pfitzner.....	Alsace-Lorraine	3.24
Yap.....	Filipinos (adults)	3.67

In the beginning of this paper I called attention to the fact that the musculus sternalis was found in different nationalities. I am inserting the following table showing this occurrence and its relative proportion in different races as reported by various writers (table 3).

The occurrence of this muscle in the two sexes is variable. In adults some authors found it more commonly in males, while others met it more frequently in females, and there are those who reported it with equal frequency in the two sexes. I found it present in adult females in the proportion of 3 to 2, in normal foetuses 1 to 1, and all the cases encountered in anencephalic foetuses were in females.

TABLE 4
*Relative frequency of musculus sternalis in the two sexes (modified after
Cunningham)*

AUTHORS	MALE	FEMALE
Bardeleben's table.....	27	25
Bardeleben.....		2
Malbranc.....	2	
Shepherd.....	3	
Le Double.....	2	1
M. Issaurat fils.....	1	
Joessel.....	1	
Dwight.....	3	3
Curnow.....	2	3
Cunningham.....	8	8
Wallace.....		1
Lamont.....		4
Turner.....	7	11
Ingalls.....	1	
Yap ¹	2	3
Total	59	61

¹ Only adult cases given.

Hallett (2) regards this muscle as inspiratory in function. Cunningham claims that if this were the case we should expect to find it present in greater proportion in females and his statistics show forty-nine males and forty-seven females, but he failed to include Turner's findings, on the ground that more females were encountered in the latter's dissecting-room. Without intending to argue the matter, we wish to call attention to our table 4 and to our previous statement regarding the preponderance of male cadavers in our dissecting-room. Moreover, we found the

muscle present in five female foetuses and in only one male, and Shepherd in five out of six female anencephalous monsters.

As to its occurrence as a double muscle in the two sexes, the same uncertainty is noted. I found it bilateral in all my female cases, while in all the male cases, except the male normal foetus, it was unilateral.

TABLE 5

Relative frequency of double sternalis in the two sexes (modified after Cunningham)

AUTHORS	MALE	FEMALE
Bardeleben's table.....	6	4
Melbranc.....	1	
Le Double.....	1	1
Joessel.....	1	
Dwight.....	1	1
Curnow.....	1	2
Cunningham.....	2	2
Ingalls.....	1	
Yap ¹		3
Total.....	14	13

¹ Only adult cases given.

In the anencephalous foetuses it was noted in much greater proportions, varying from 16 to 88 per cent. I found it present in my series in about 40 per cent. There is as yet no definite explanation advanced to account for this frequency of occurrence. Shepherd (4) seems to believe that it points rather to its being a rudiment than a new muscle:

Windle (cited by Ruge (3)) comes forward with the suggestion that the muscle might be found in greater proportion in lunatics, evidently basing his belief on the frequency of its presence in anencephalous monsters. He does not, however, attempt to offer any basic reason for such suggestion. We cannot at present advance any opinion on this aspect of the subject; we wish, nevertheless, to call attention to the high percentage of the musculus sternalis (40 per cent) in the anencephalous foetuses examined by us, and the fact that out of five adults which showed the muscle in our series, two were chronic insanes and two were

criminals. It would seem that this point might be further looked into with a view of explaining the connection between this anomaly and insanity, if there is really such a relation.

TABLE 6
Musculus sternalis in anencephalic fetuses (modified after Ruge)

AUTHORS	NUMBER OF CASES	NUMBER OF TIMES FOUND	PERCENTAGE
Shepherd.....	9	8	88.0
Eisler.....	7	4	57.0
Abraham.....	11	6	54.0
Windle.....	27	10	37.0
Cunningham.....	6	1	16.6
Yap.....	10	4 ¹	40.0
Total.....	70	33	47.14

¹ Double.

The homology of the musculus sternalis is as yet a question that remains unsettled. Anatomists who have given extensive accounts of the muscle vary in their views. Some based their conclusions chiefly from its connections, while others took into consideration its nerve supply, and there are those who look upon it as a muscle sui generis and peculiar to man. There are at present five hypotheses of interest regarding the homology of this muscle:

1. That the muscle is a remnant of the paniculus carnosus and associated in man with the platysma myoides.

This theory is ably and extensively discussed by Professor Turner (1), whose views are shared by Hallet, Parson, Lambert (3), and a few others.

Turner seems to base his conclusions on these observations:

- a. That in muscular subjects the platysma myoides descended over the clavicle and above the pectoralis major for a considerable distance (2 to 4 inches) on the anterior surface of the chest.

- b. The fact that occasionally portions of the paniculus carnosus, besides the platysma and the palmeris longus, are found in other parts of the body.

c. The occasional crossing of the platysma myoides in front of the sternum as observed by Teichmann, resembling in such cases the position assumed sometimes by the musculus sternalis.

d. That in lower animals the paniculus carnosus is well developed in the ventral surface, and extends with a marked process over the pectoralis major.

There are two points which in our mind speak against the above hypothesis:

a. The fact that the platysma is found in the superficial fascia, whereas the musculus sternalis is under it, so that the two muscles are in two distinct morphological planes.

b. And the other, as Cunningham (2) points out, is the innervation of the muscle. He correctly reasons that if the muscle were a part of the paniculus carnosus, we should expect it to be innervated by a special branch from the brachial plexus, whereas all the observations reported so far indicate that it derives its nerve supply from the anterior thoracic nerves or the intercostals.

Parson (3), in his work on rodents, claims that the musculus sternalis may be the persistence of the deeper layer of the pectoral section of the paniculus carnosus. But here again the nerve supply of the muscle speaks against this view.

2. Albinus (1) first advanced a theory which regards the musculus sternalis as an upward extension of the rectus abdominis muscle. Turner, however, claims that in all those mammals where the rectus abdominis is prolonged upward, the fibers of the prolongation were always encountered under the great pectoral muscle and in contact with the ribs, whereas the musculus sternalis in man is always found superficial to the pectoralis major.

3. Bourienne (3) is responsible for the theory which regards the musculus sternalis as a downward prolongation of the sternocleido mastoid muscle. He was later supported by Henle, Marjolin, Gegenbaur, Theile (3), and others. It is a point of common observation that the sternal origin of the sternomastoid is in common with the insertion of the musculus sternalis. I found this to be the case in five out of eleven cases and Turner in thirteen out of twenty one. Cunningham (2), in discussing this view, says that if the musculus sternalis were a part of the

sternomastoid, we should expect it to be innervated by some branch of the spinal accessory or the cervical plexus, which occurrence, however, has never been reported. Ruge (3) claims that in no animals the sternomastoid extends to the abdomen or to the aponeurosis of the external oblique, and that, furthermore, the innervation of the musculus sternalis is against the above theory.

As modifications of the above two hypotheses we also find the following views:

a. Testut with Anthony (3) believes that the upper part of the musculus sternalis belongs to the sternomastoid, while its lower portion is a part of the external oblique muscle. This contention is based upon the claim that these two muscles (sternomastoid and external oblique) are in the same morphological plane and "that the musculus sternalis is the remnant in man of the old connection which formerly existed between the two, a connection which exists in serpents." Cunningham (2), however, contends that such a connection becomes the pectoralis major in the thrusting out of limbs. Besides, we must remember that serpents are not philogenetically related to mammals.

b. Bardeleben (2) claimed that the musculus sternalis when receiving its nerve supply from the intercostals must be considered as belonging to the sternomastoid, and when innervated by the anterior thoracics to the pectoral group.

Cunningham (2) takes exception to this view, on the ground that in the majority of cases which he recorded as supplied by the anterior thoracic nerves, the muscles were directly continuous with the sternomastoid. This fact was confirmed by us in five of our cases; furthermore, there are cases in which musculus sternalis, though innervated by the intercostals, were not continuous with the sternomastoid.

4. That the musculus sternalis is a muscle sui generis and peculiar to man, without a representative in lower animals. This view was advanced by Professor Halbertsma (1).

5. The musculus sternalis belongs to the pectoral group of muscles. This last view was first advanced by Bardeleben, who claimed that a certain proportion of the muscles could be considered as portions of the pectoralis major.

Abraham (2) applied this view more extensively. He considered all sternal muscles without exception as aberrant portions of the great pectoral.

Cunningham and Shepherd, on the strength of the innervation of the muscle by the anterior thoracic nerves, strongly support the above view. Their finding has been confirmed by other observers and we have also verified it in six cases.

The above authors further contend in favor of this theory the fact that some fibers of the musculus sternalis in some instances appeared directly continuous with the pectoralis major. Such instance was encountered several times in our series.

Another point which might also be mentioned in support of this hypothesis is the presence of a gap or deficiency in the fibers of the great pectoral at the lateral side of the musculus sternalis.

Such occurrence was reported by Shepherd in four of his cases and we have met it once in our study. We agree with Cunningham when he said, "it is reasonable to suppose that the gap is caused by the abstraction of this portion of the muscle to form the sternalis and there are many cases figured which would lead one to suspect that the rotation of fibres has taken place in an upward and inward direction."

The above explanation would surely account for those cases where the lower end of the muscle lies under cover of the great pectoral. Ruge, after an extensive discussion of the above different theories is inclined to agree with Cunningham that the sternalis is probably a portion of the pectoralis major.

Our present study inclines us to agree with the preceding explanation of the homology of the muscle. We have found the muscle supplied by the anterior thoracic nerves in six out of eight cases; we met it in close relationship with the pectoralis major and in several cases there was a direct muscular connection between the two, either in the points of origin or at the ends of insertion, and finally we also found one case where a decided gap was seen in the pectoralis major just lateral to the sternalis.

Furthermore, we quote the following from Lewis (6) on the formation of the pectoralis major: "The pectoralis major early splits into a series of overlapping bundles, and during the migra-

tion of the muscle the superficial fibres of each bundle move farther caudally than the deeper ones, giving the overlapping condition found in the adult."

It will not be too far fetched to suppose that sometimes some of the superficial fibers split from the pectoral muscle mass and fail to migrate caudally with the rest, forming in that manner the narrow sternalis muscle.

We wish to express our indebtedness to Dr. Otto Schobl, of the Bureau of Science, for kindly helping us in the translation of some of the literature.

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PLATES

PLATE 1

EXPLANATION OF FIGURES

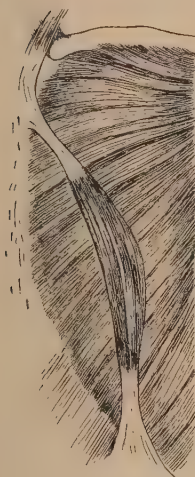
Drawings by Vicente Santos

Case I Male, 36 years. Musculus sternalis unilateral, left. Origin: Pars abdominalis of left pectoral major at level of sixth rib. Insertion: Second costal cartilage blending with pectoralis major and sternomastoid. Nerve supply: Medial anterior thoracic.

Case II Female, 85 years. Musculus sternalis bilateral. Origin: (Both) pectoralis major at level of fourth rib. Insertion: Anterior surface of sternoclavicular joint blending with corresponding sternomastoid. Nerve supply: Anterior thoracic.

Case III Female, 89 years. Musculus sternalis bilateral. Left muscle, shorter and smaller. Origin: Left rectus sheath and sixth rib. Insertion: Manubrium sterni at level of second rib. A tendinous slip from this unites with the tendon of the right muscle. Nerve supply: Anterior thoracic. Right muscle: Origin: Right rectus sheath and sixth rib. Insertion: In common with the sternal origins of the two sternomastoid. Nerve supply: Anterior thoracic.

Case V Male, 20 years. Musculus sternalis, unilateral, right. Origin: Fascia covering lower portion of pectoralis major. Insertion: Upper tendon to manubrium sterni; lower tendon to body of sternum at level of third rib. Nerve supply: Intercostals.



Case I



Case II



Case III



Case V

PLATE 2

EXPLANATION OF FIGURES

Drawings by Vicente Santos

Case VI Normal foetus, female. *Musculus sternalis*, bilateral. Right muscle: Origin: Sixth costal cartilage and costal origin of *pectoralis major*. Insertion: Continuous with the right *sternomastoid*. Nerve supply: Lateral anterior thoracic nerve. Left muscle: Origin: Aponeurosis of external oblique, rectus sheath, and costal portion of *pectoralis major*. Insertion: Sternal portion of *pectoralis major* at level of second interspace and to the right *pectoral major* at level of second rib. Nerve supply: Not identified.

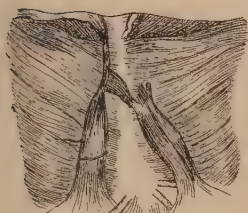
Case VII Normal foetus, male. *Musculus sternalis*, bilateral. Right muscle: Origin: Costal portion of *pectoralis major* at level of fifth interspace. Insertion: Sternal portion of great pectoral at level of third rib and to the *sternomastoids*. Nerve supply: Not found. Left muscle: Origin: Sixth rib and adjoining portion of the *pectoralis major*. Insertion: To both mastoid muscles. Nerve supply: Not found.

Case VIII Anencephalous monster, female. *Musculus sternalis*, bilateral. Right muscle: Origin, aponeurosis of external oblique muscle and pars abdominalis of the great pectoral. Insertion: Lower portion of manubrium and to second cartilage. Nerve supply: Medial anterior thoracic. Left muscle: Origin: Costal portion of *pectoralis major* and by a small slip from the middle part of the muscle. Insertion: Lower portion of manubrium and upper portion of the body of the sternum. Nerve supply: Not found.

Case IX Anencephalous monster, female. *Musculus sternalis*, bilateral. Right muscle: Origin: Pars abdominalis of great pectoral; Insertion: Sternal portion of right *pectoral major* at level of third rib. Nerve supply: Medial anterior thoracic. Left muscle: Origin: Aponeurosis of external oblique. Insertion: Third costal cartilage and in common with the right *musculus sternalis* into the sternal part of the great pectoral muscle at level of third rib. Nerve supply: Medial anterior thoracic.

Case X Anencephalous monster, female. *Musculus sternalis*, bilateral. Right muscle: Origin: Rectus sheath and aponeurosis of external oblique. Insertion: Sternal portion of great pectoral at level of second interspace and into sternal portions of the two pectorals at median line. Nerve supply: Third intercostal. Left muscle: Origin: Costal portion of great pectoral at level of fifth rib. Insertion: Sternal portion of great pectoral at level of upper border of third rib. Nerve supply: Not found.

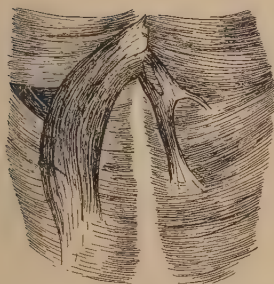
Case XI Anencephalous monster, female. *Musculus sternalis*, bilateral. Right muscle: Origin: Aponeurosis of external oblique and abdominal portion of great pectoral. Insertion: Manubrium sterni and anterior part of the sterno-clavicular joint. Nerve supply: Not found. Left muscle: Origin: Sternal portion of great pectoral at level of fourth costal cartilage. Insertion: Upper border of the manubrium sterni. Nerve supply: Not found.



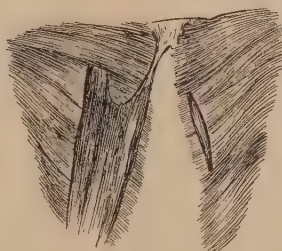
Case VI



Case VII



Case VIII



Case X



Case IX



Case XI

Resumen por el autor, Charles W. Metz.

Un sencillo método para manejar objetos pequeños durante la obtención de preparaciones microscópicas.

Para preparar objetos muy pequeños con el fin de obtener cortes, el autor ha encontrado muy útil el empleo de la piel que rodea el abdomen de las ninfas de la mosca de los frutos, *Drosophila*. Separando la cubierta ninfal, para lo cual se separará el abdomen del resto de la ninfa, y comprimiendo dicha cubierta se obtiene un pequeño saco transparente en el cual pueden introducirse los objetos que se desea preparar. Este saco puede llenarse durante la fijación o antes de depositar los objetos en el alcohol de 70. Se puede obtener un gran número de ninfas exponiendo al aire frutas fermentadas, y las cubiertas pueden guardarse hasta el momento de usarlas en alcohol de 30 o 50 grados. Si se emplean ninfas de varias especies pueden obtenerse cubiertas de diversos tamaños.

Translation by José F. Nonidez
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A SIMPLE METHOD FOR HANDLING SMALL OBJECTS IN MAKING MICROSCOPIC PREPARATIONS

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In the course of cytological studies on flies, especially *Drosophila* and other small forms, I have met with considerable difficulty in transferring the very small gonads during the processes of fixing, washing, dehydrating and embedding. After trying various methods of handling these objects the following was worked out and has proven so satisfactory that I am led to make a brief record of its essential features.

The method is similar to the well known one of wrapping the objects in *Cryptobranchus* epidermis or some other transparent membrane; but instead of a flat sheet of tissue it utilizes the bag-like skin surrounding the abdomen of the *Drosophila* (fruit fly, vinegar fly, banana fly) pupa. At about the middle of the pupal stage the abdomen of a *Drosophila* is covered with a thin, transparent skin, under the chitinous pupa case. The skin may be obtained intact by cutting the pupa in two across the thorax, removing the posterior part from the case and pressing out the contents. A simple procedure for this is to puncture the pupa with a needle about a third of the way back from the anterior end (end with the long 'horns'), then transfer it to water and tear it in two with dissecting needles, after which the abdomen and the attached portion of the thorax may easily be pulled or pressed from the pupa case and their contents removed by gentle pressure with a needle. The latter is facilitated if the apex of the abdomen is held down with the point of the other needle.

An oval, transparent bag remains, having a somewhat constricted opening at the anterior end representing the connection between abdomen and thorax. The small objects to be treated may be passed through this into the pouch until the latter is

nearly full and then the opening may be closed by pressing or twisting the edges together with needles or forceps and immersion in the fixative or alcohol. I have usually fixed and washed the objects and run them up to 50 per cent alcohol before packing them into the pupa-skins. This obviates the necessity of leaving them long in the dissecting fluid during the dissecting and packing into the pouch. But with other objects such as small eggs, etc., which do not involve much dissection, or when such exposure to the dissecting fluid is not injurious, the packing may be done before fixation.

Once a packet is made in this manner and the membrane has hardened in the alcohol or fixative it may be handled readily without fear of losing the contents. Reagents, including paraffin, penetrate the membrane readily, so that dehydrating and embedding may be done rapidly. Since it is easy to secure species of *Drosophila* of various sizes around garbage, decaying fruit, etc., it is possible to obtain pupa-skins of sizes adaptable to individual needs. By putting a few flies in a cotton-plugged bottle with ripe banana (or something similar) and a little paper, practically any desired number of pupae may soon be obtained. The pupa-skins may be prepared as noted above and kept in 30 per cent or 50 per cent alcohol until needed. Thus a supply sufficient for months or years may be made up at one time.

At first this method seems somewhat tedious, but with a little practice it proves to be rapid and efficient. Among its favorable features may be mentioned, 1) standardization of size of packets, 2) convenience of size of packets, 3) minimum amount of enclosing tissue together with close aggregation of objects within, making it unnecessary to section a packet much larger than the mass of objects themselves—a considerable saving—4) transparency of the enclosing membrane at all stages, permitting orientation or examination of the contents, 5) cleanliness of membrane and freedom from dirt or grit such as is often encountered in amphibian epidermis, and 6) relative freedom from extraneous tissue or material in the sections, thus facilitating their examination.

Resumen por el autor, Lee D. Cady.

Un estudio microscópico del fascículo senoventricular del corazón del conejo, con referencia a los datos relativos a su interpretación funcional, especialmente en términos de un manantial de reemplazo del miocardio degenerado.

El nodo del seno y el nodo atrioventricular son prácticamente idénticos en estructura histológica en el conejo. En estos nodos puede observarse la presencia de numerosos núcleos en varios estados de división amitótica, pero los núcleos de las células binucleadas están colocados muy próximos entre sí y no existe prueba de la división protoplásmica. La porción principal del fascículo atrioventricular presenta una estructura muy semejante. En las fibras de Purkinje, sin embargo, los núcleos están más separados que en las porciones del sistema conductor situado más encima. En las áreas de transición entre las fibras de Purkinje y el miocardio ventricular, se encuentran tan solo núcleos impares. En el tejido nodal o en el tejido del fascículo no existe indicio alguno que indique la división citoplásmica de las células, ni tampoco hay dato histológico que indique un reemplazamiento de las fibras miocárdicas degeneradas por una progresión genética de las células a partir del nodo del seno hacia el miocardio ventricular.

Translation by José F. Nonidez
Cornell Medical College, New York

A MICROSCOPICAL STUDY OF THE SINOVENTRICULAR BUNDLE OF THE RABBIT'S HEART; WITH REFERENCE TO THE DATA RELATIVE TO ITS FUNCTIONAL INTERPRETATION, ESPECIALLY IN TERMS OF A SOURCE OF REPLACEMENT OF DEGENERATED MYOCARDIUM

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ONE PLATE (FIVE FIGURES)

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INTRODUCTION

This study of the sinoventricular bundle was undertaken with the view of testing Retzer's ('20) recent rather startling conclusion that worn out myocardium is replaced from the sinus region of the heart, the new myocardial fibers being derived from the Purkinje fibers, which in turn are said to be derived from higher regions of the sinoventricular system. He compares the sinus region to the basal layer of cells in stratified (transitional) epithelium in that both of them are differentiated in the embryo, and he thinks that the sinus cells continue to multiply in a manner analogous to the manner in which the basal cells of stratified epithelium multiply in adult life. In 1908 Retzer expressed his belief that the Purkinje fibers are derived from the sinus tissue, but said nothing about a possible derivation of myocardial fibers from the Purkinje fibers. Retzer's conclusion is based for the most part upon a study of the pig's heart.

That there is a direct transition between the Purkinje fibers and the myocardial fibers was shown by Tawara ('06), and confirmed by Retzer ('08), Lhamon ('12), DeWitt ('09), and others, who traced the Purkinje fibers to their transition into cardiac fibers; but none mentioned indications of a possible replacement of degenerated myocardial fibers from that source.

This paper is concerned with the study of the rabbit's heart only with reference to the sinoventricular bundle, as Retzer terms the entire conduction system from sinus to Purkinje fibers, inclusive, and purports to present the data as found in the material studied with reference to its functional interpretation, especially as regards the replenishment of worn-out myocardial fibers by the sinoventricular bundle. No attempt was made to study the 'right lateral connection' of the atrioventricular junction, as Kent ('13) calls it, for its functional existence has apparently not been substantiated (Erlanger, '08). Retzer ('08) describes it in the pig's heart. We have been unable to find any really clear clinical demonstration that such a connection exists, and the experiments of Erlanger and Blackman ('10) show conclusively that there is either no such connection or that, if there is such a connection, it does not function as a pathway of conduction when there is greatest physiological need for it, namely, when the sinoventricular system is destroyed.

MATERIALS AND METHODS

The heart of the rabbit shows the conductive system with extraordinary detail in routine preparations from some of the specimens, there being some variation in this respect. About twenty rabbits' hearts were studied. They varied in age from one week to the well-matured specimens that can be found in the ordinary animal room. Sections were also kindly furnished by Dr. H. E. Jordan, which were invaluable in carrying out this work. Altogether something over three thousand sections were examined.

Details regarding technique were taken from Jordan's 'Text Book of Histology' ('20). A variety of fixing methods were used, including Flemming's, Meves', Zimmermann's, Zenker's,

Zenker-formol, 95 per cent alcohol, and 10 per cent formalin. One adult heart was opened by a longitudinal incision through the lateral wall of the right atrium and the cut continued down through the ventricle until the apex was reached. The parts of the lateral walls of both atrium and ventricle were then pulled aside and the whole heart flattened with thin strips of cork against a clean glass slide, weighted down in that condition with light weights, and covered with Zenker-formol fixing fluid. By this method it was possible to include in the longitudinal sections of the heart longer sections of the conductive system. A one-week-old heart, fixed in 95 per cent alcohol, was sectioned transversely; i.e., at right angles to the long axis of the heart. The sections were mounted serially and stained with hematoxylin and eosin. The atrial septum of a young adult, likewise fixed in 95 per cent alcohol, was sectioned longitudinally and mounted serially, beginning with the endocardial surface of the left atrium, and stained with hematoxylin and eosin. These sections were designed to show the nodal tissue. Blocks of the septum and of the walls of both ventricles were sectioned longitudinally, in order to get longitudinal and oblique sections of the transition areas of the Purkinje fibers. The material furnished by Doctor Jordan, a celloidin preparation, fixed in Zenker's fluid, was cut transversely, and stained with hematoxylin and eosin.

All serial sections were mounted five or six to the slide, and the sections on alternate slides were stained with hematoxylin and eosin, while the remaining sections were stained either with iron hematoxylin and picro-fuchsin or by other special methods, including Mallory's phosphotungstic acid-hematoxylin. Blocks of tissue from two hearts were stained with hemalum after Zimmermann fixation for intercalated discs. Silver impregnation methods were also used. All sections were mounted in Canada balsam.

DESCRIPTION

Keith and Flack's ('06) description of the sinus node in the human heart agrees closely with what is found in the rabbit's heart. They describe the nodal fibers as striated, of fusiform shape, with well-marked elongated nuclei, plexiform in arrangement, and imbedded in densely packed connective tissue—in fact, of a structure very like that of the atrioventricular node. There is slightly more connective tissue in the atrioventricular node in our sections than in the sinus node (figs. 1 and 2), but this tissue is not abundant enough to warrant the description as 'closely packed.' The nuclei could hardly be described as 'well-marked elongated nuclei,' for they are more nearly oval. A careful comparative study of the two nodes in the sections fails to reveal any distinct difference other than those already mentioned. They further state that these two nodes resemble each other in other mammalian hearts, the resemblance being especially marked in the mole, rat, and the ram. To this enumeration we can add that they are practically identical in appearance in the rabbit.

In the atrioventricular node (fig. 2) and the sinus node (fig. 1) the cross-striations of the fibers appear only very faintly in some of the hearts. In others the striation is more conspicuous. The myofibrils are peripherally placed; the nuclei are located centrally and they are surrounded by a relatively large amount of undifferentiated sarcous material which is rather granular. Frequently, however, in the regions of the nuclei there is no evidence of granules in the stained sections. Only rarely can one find any fibrils immediately adjacent to the nuclei. The nuclei are large, oval, and rather vesicular in appearance. They contain scattered granules of chromatin material which, except for a few chromatin clumps, is pretty evenly distributed. Many of the nuclei show one or two nucleoli. Frequently one finds two nuclei, rather smaller and more heavily stained than the larger single nuclei within the same perinuclear spaces and in close juxtaposition. No evidence of mitotic division can be seen in the cells of either of these nodes. Connective-tissue cells are scattered rather sparsely throughout the sectioned surfaces of

either node, but slightly more connective tissue is in evidence in the atrioventricular node. There seems to be no definite connective-tissue sheath surrounding either node. The nodal fibers of the sinus pass by gradual transition into the atrial fibers and are soon lost in them. The two nodes resemble each other so closely that one is safe in saying that they are identical in appearance, for, unless one knows the exact region of the section, it is impossible to identify either node with any degree of certainty except by the relative amount of connective tissue, which is in itself a variable (Cohn, '09).

The cells of the sinoventricular bundle below the region of the sinus node, that is, in the atrioventricular node, have very well-defined boundaries (fig. 3). The cytoplasm in stained sections appears pale, and in many of the cells shows only slight differentiation. The cell peripheries stain more deeply than the remainder of the cytoplasm, and at the levels of the nuclei show peripherally placed myofibrils, which are finer than those of the myocardial fibers. The nuclei are usually situated in relatively large clear areas and in the central portion of the cells. In fact, the large clear central area is the most conspicuous feature of these cells. The nuclei are rather pale, but well stained. Chromatin granules are fine and pretty evenly distributed, but nuclei are easily found that show chromatin clumps as in the atrioventricular node. Well-defined nucleoli, which take a pink stain in the hematoxylin and eosin preparations, are found in the nuclei; indeed, many nuclei show from two to four nucleoli. A large percentage of the cells have two nucleoli.

One cell was noticed that appeared to have four nuclei within the same perinuclear space. Where there are two nuclei, they are usually somewhat smaller than the nuclei in the mononucleated cells and they are darker in appearance. The binucleated cells also have nuclei that closely resemble the single nuclei in size, shape, and staining reaction. This type of nucleus is generally less closely apposed to its fellow than are the smaller and darker nuclei, which are usually somewhat flattened against each other. Nuclei in the various stages of amitotic division are frequently seen. However, no cells were seen that had their

nuclei widely separated or showed evidence of cytoplasmic division. No mitotic figures were seen in any portion of the system. The bundle is separated from the ventricular myocardium by means of a thin connective-tissue sheath. Connective-tissue cells are found also scattered throughout the entire bundle. The bundle has a subendocardial position everywhere except in the moderator band and in the so-called 'false tendons.'

In the case of the moderator band and of the false tendons (fig 3) the above description of the bundle also applies except that these particular subdivisions of the sinoventricular bundle are still further subdivided by connective-tissue septa, delicate in the moderator band, relatively robust in the false tendons, where the larger strands of the bundle are enveloped by relatively dense connective-tissue sheaths.

The Purkinje fibers (figs. 4 and 5) are only slightly more differentiated than the bundle cells. The nuclei are of about the same size and appearance as those of the bundle except at the points of transition into the myocardial fibers where they are smaller and gradually pass over into the myocardial type of nuclei. As the transition areas are approached, the binucleated cells become progressively fewer until the transition area is reached, where only unpaired nuclei are found. The cytoplasmic transition is more gradual than that of the nuclei, and it is almost impossible to determine just where Purkinje fibers actually end and the myocardial fibers begin. The Purkinje fibers are larger than the myocardial fibers, but at the transition points they diminish in diameter gradually and take on a more conspicuously striated and fibrillated condition. The connective-tissue sheath of the Purkinje fibers is very delicate and often does not show, especially at the transition points.

DISCUSSION

To answer the question whether the sinoventricular bundle consists of embryonal tissue and whether it may be able to differentiate into myocardium, one must consider its histogenesis. The cells of the sinoventricular bundle are differentiated early in embryonic life (eleven weeks in Keith's human embryo). The

facts that their myofibrils are more delicate and more peripherally placed and less conspicuously striated than in the myocardium and that there is more undifferentiated sarcoous material centrally in these cells do not argue conclusively that they are embryonic cells. Their large size, their variously stout fusiform, polyhedral, and irregular shapes, and their striated fibrillar structure, all jointly indicate that they are specialized cells. Lange ('14) arrives at the conclusion also that the Purkinje fibers are not embryonic remains, since they are clearly distinguishable in very young mammalian hearts. He concludes further that they are a non-nervous apparatus for conducting the impulse to heart beat. The most suggestive evidence in favor of Retzer's conclusion relates to his observation that in the cells of the terminal portions of the bundle the nuclei have moved relatively farther apart. But this fact may be equally plausibly interpreted as the result of a secondary (mechanical) elongation of the cells of this region consequent to the imposition of stresses during the growth of the heart.

Howell ('19) states that it is uncertain whether the atrio-ventricular bundle contracts during systole, but that there is little doubt as to its function of conduction of the impulse to heart beat. Intercalated discs are not found in the atrio-ventricular bundle, but they are present in the Purkinje fibers (Jordan, Banks, '17). They occur very early in fetal life in the myocardium, during the second month in the heart of the beef (Jordan, Banks, '17). Assuming that intercalated discs are modified irreversible contraction bands produced through functional strains and stresses, we come to the conclusion that the atrioventricular bundle either does not contract, or at least, if it does contract, it does not share the strains ordinarily incident to heart beat, and that the Purkinje fibers do contract. However, the cells of the bundle show cross-striation, which is in itself an indication of their muscular nature. Curran's ('09) conclusion is that the presence of the constant bursa (interpreted by Lhamon ('12) as a connective-tissue sheath and not as a bursa) which he describes surrounding the atrioventricular bundle indicates that this muscle bundle either does not contract at all or that it con-

tracts in a different way and at a time which is not synchronous with the contraction of the ventricular myocardium, and he inclines to the latter view. His observation on a beating heart lead him to believe that the atrioventricular bundle contracted synchronously with the atria, but his observation was not confirmed by graphic methods. Erlanger ('12) was not able to demonstrate any contraction in excised segments of false tendons even when they were perfused through their own blood vessels with various solutions. The fact that there are no intercalated discs in the atrioventricular bundle does not prove that it does not contract, nor does the fact that there are cross-striated myofibrils in the bundle prove that it does contract. Embryonic hearts, and tissue cultures from embryonic chick hearts, exhibit rhythmical contraction before intercalated discs or the full complement of cross-striations appear. Cross-striations are apparently not necessary for contractility in heart muscle. Doctor Burrows kindly made it possible for us to examine some of his tissue-culture preparations of embryonic chick hearts ('12). We found no intercalated discs nor cross-striations, but only irregularly arranged myofibrils within the sarcoplasm. These preparations were known to have shown rhythmical contraction for relatively long periods of time. It may be possible that the sinoventricular bundle conducts the impulse to heart beat and still does not itself contract. If the calcium be removed from one end of a strip of myocardium and that end be stimulated, it will conduct the impulse for contraction to the untreated end, which immediately contracts, but the treated end will not contract. A knowledge of the calcium content of the bundle would be interesting in this connection. However, the only conclusive method of determining whether or not the bundle tissue contracts is to study its activity, if any, by improved graphic physiological methods.

If Retzer's unique conclusion that the myocardial fibers are replenished from the sinoventricular bundle is correct, it is very difficult to reconcile this interpretation with the facts disclosed by pathological and experimental data. Keith and Miller ('06) reported a case of syphilis of the heart where the superior

vena-cava region of the atrium, the coronary sinus, and the atrioventricular node had been destroyed about thirteen years before death. ". . . the muscular connection between auricle and ventricle had been destroyed several years (probably 13) before death, yet the complete section of the bundle had not resulted in any visible atrophy beyond the point of destruction. Were this peculiar system, . . . only a conducting pathway for the auricular stimuli into the ventricle, one would expect degeneration in the system of fibers beyond the point of section, for it may be taken as an axiom in biology that abrogation of function is invariably followed by atrophy." This heart showed no signs of failure or patent symptoms of cardiac insufficiency once the patient had recovered from the symptoms incident to the onset of his bradycardia (about forty-two beats per minute) until his death twelve years later as a result of acute peritonitis. If the heart muscle does constantly receive new fibers from the sinoventricular bundle, it is reasonable to expect that there would have been more pronounced symptoms of cardiac insufficiency after the relatively long time that the ventricles had no connection with the sinus region. Furthermore, if there were a constant genetic progress of cells from the sinus to the ventricular myocardium, there would certainly have been marked changes in the myocardium, which were absent in this heart; and especially would there have been profound changes in the part of the conduction system below the lesion. Neither atrophic nor hypertrophic changes are mentioned occurring in the ventricles, nor is either change shown in the sketches accompanying the report. If there were no such changes resulting from the above-described lesion, such would be indirect evidence that the number of cardiac muscle fibers in the adult was the same as the number laid down at birth as stated by MacCallum ('98) and direct evidence against a replenishment of the myocardium from the sinoventricular bundle; for there was no atrophy in the part of the sinoventricular bundle below the lesion. Retzer himself was unable to find any histologic evidence of a degeneration of myocardium in many normal hearts examined.

Keith and Flack ('06) confirmed Tawara ('06) in his finding that this system neither enlarges with cardiac hypertrophy nor diminishes in size with atrophy. Beck and Stokes ('08) and Cohn and Lewis ('12), record the same findings as Keith and Miller as regards failure of the bundle to atrophy beyond a lesion. Erlanger and Blackman ('10) find that this system does not regenerate after its experimental destruction.

Through the kindness of Doctor Erlanger, we have had the opportunity of examining the sections of the ventricular septum of dog no. 8 described in his article to which we have just referred. There is no abnormality above the scar, no regeneration through or around the scar, and no atrophy below the scar. The atrio-ventricular bundle was almost but not quite completely crushed, as shown by the sections. It would seem that conditions here were favorable for at least a partial regeneration, but none occurred. This dog lived for three months and had complete heart-block up to the fifteenth day. From the fifteenth to the forty-second day the block was incomplete. Thereafter the block again became complete and remained so until the death of the dog. Erlanger and Blackman believe that this variable condition may be accounted for by the subsidence of inflammatory processes so that about the fifteenth day physiological connection was again partially established, but that on about the forty-second day the contraction of the scar tissue again broke the partial physiological continuity of the bundle, and again caused complete heart-block.

As regards the regeneration of the sinoventricular bundle, all the evidence shows that it does not regenerate after injury. This fact is also true of all cardiac musculature. Erlanger ('08) crushed the musculature of the atrial appendix in a carefully controlled and aseptic experiment. He found that there was no attempt at regeneration on the part of the myocardial fibers, but that nerve fibers readily regenerated across the contused area. Inasmuch as the atrioventricular bundle is known to be as much a part of the primitive heart as is the myocardium itself (Erlanger, '12) we would hardly expect any difference in this regard between them.

SUMMARY

1. The sinoventricular bundle is not embryonic muscle tissue. It would appear to be a specially differentiated tissue with the definite function of conduction of the impulse to heart beat.

2. There is no adequate histologic evidence in support of the suggestion that worn-out myocardium is replaced from the sinoventricular bundle.

3. Whether or not the sinoventricular bundle has retained the fundamental property of contractility is not to be determined by histological study; it must be determined by improved graphic physiological methods.

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PLATE

PLATE 1

EXPLANATION OF FIGURES

1 Drawing of a section of the sinus node taken parallel to the long axis of the right atrium. The nuclei are large, oval, or elongated, with a random distribution of fine chromatin granules and several nucleoli. Some cells are binucleated. The cytoplasm shows large perinuclear spaces. Striated myofibrils are distributed around the periphery of the cells. $\times 780$.

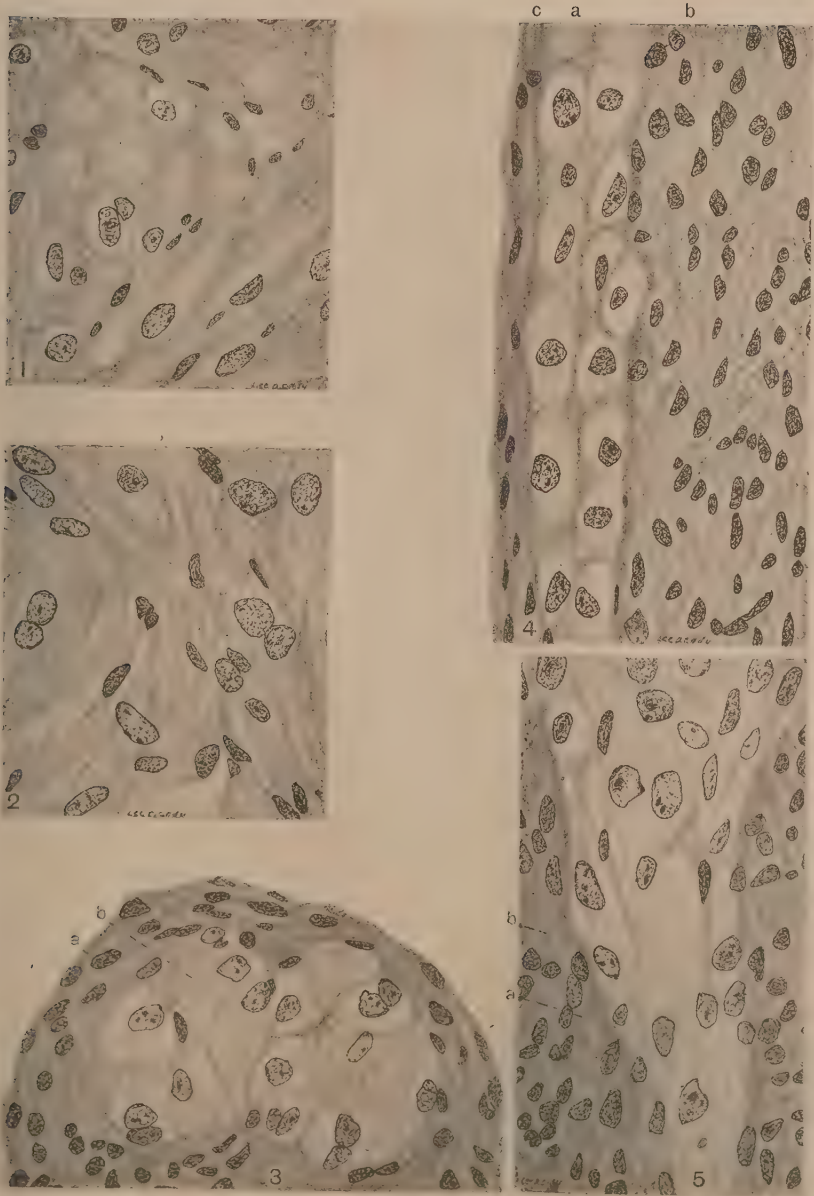
2 Drawing of a section of the atrioventricular node taken parallel to the long axis of the heart. Description same as in figure 1.

3 Drawing of a section of a false tendon cut at right angles to the long axis, showing: (a) The sinoventricular bundle tissue with the characteristic large oval or elongated nuclei. Many of the cells are binucleated, and the nuclei are closely adjacent to each other. The cytoplasm is pale and contains fine myofibrils in the cell peripheries. (b) Endocardium and connective-tissue sheath. $\times 780$.

4 Drawing of Purkinje fibers (a) in cross-section, showing relative differentiation as compared with adjacent ventricular myocardium (b). The nuclei are larger, paler, and more nearly oval. The perinuclear spaces are much larger than in the myocardium. The myofibrils are fewer, finer, and paler, and placed more peripherally than in the myocardial fibers. (c) Endocardium. $\times 780$.

5 Purkinje fibers in oblique section, showing gradual transition (a) into myocardial fibers (b). The nuclei gradually change in character from the typical Purkinje nuclei to the typical myocardial nuclei. The myofibrils gradually converge and pass insensibly into the myocardial fibers. $\times 780$.

All drawings are from hematoxylin and eosin preparations.



Resumen por el autor, R. Bennett Bean.

Observaciones sobre la enseñanza de la Anatomía.

I. Introducción. El profesor y el estudiante son más importantes que el método seguido, y la investigación es necesaria por parte de ambos. La anatomía comparada y la embriología deben requerirse como los fundamentos de la anatomía. El autor enumera algunos de los métodos seguidos por otros profesores, aconsejando la combinación de lo científico y lo práctico. Los estudiantes y las tradiciones difieren según las escuelas; los métodos empleados en una pudieran no ser útiles en otra. II. Métodos propios. (1) Cuadros murales de las partes fundamentales de los sistemas linfático, nervioso, simpático, alimenticio y arterial, con reconstrucción por los estudiantes son importantes para adquirir un conocimiento de conjunto más bien que un conocimiento fragmentario de la anatomía. (2) Los estudiantes aprenden los detalles y las relaciones al demostrar las partes disecadas a los instructores. (3) Un curso avanzado de anatomía aplicada con preguntas y demostraciones enseña al estudiante la manera de expresarse, y hace resaltar las partes importantes, especialmente la función y las aplicaciones para estudios futuros. (4) La Antropología se usa como un fundamento y un accesorio importante en la enseñanza de la anatomía. III. El autor ha enseñado tres tipos de la raza blanca, hiper y meso, braquiskele y macroskele, carnívoro y herbívoro en relación con los modos de variación, de carácter de la mente, y de la inmunidad y susceptibilidad para la enfermedad, durante los diez últimos años. Los tipos físicos han sido ya establecidos; los tipos psíquicos, fisiológicos y patológicos están aún en el umbral. La Antropología y la Psicología debían estar en la misma base que la Anatomía, fisiología, cirugía o cualquier otra parte un plan de estudios médicos bien repartido.

REMARKS ON TEACHING ANATOMY

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Many methods have been devised for the teaching of anatomy, and inasmuch as any method may succeed in suitable environment, the suggestion of other methods will give a wider range for selection. Choice of the best from the wide experience of the many, through trial and error, may ultimately result in a perfected system. Reticence is therefore not a commendable virtue, hence the present scattered remarks.

The teacher and the student, who are the two active elements in all teaching, do not depend so much upon method as upon the teacher and the student. Given fitness in both, and the task is half done. And the method that works well under certain conditions may not work well under others. Teachers and students vary.

The value of research is generally recognized as a prime requisite for the teacher of anatomy, and the attitude of the student should be that of a discoverer. A journey of exploration is to be conducted into the unknown. It were folly to attempt such a journey without guide or compass or without previous experience. Courses in comparative anatomy and embryology are as necessary to fit the student for the highest expression in anatomy as courses in Greek, Latin, and Anglo-Saxon to fit the student for the highest expression in English; yet the one is about as rare as the other.

The size and complexity of the human brain cannot be appreciated without having studied the brains of a series of animals; the homologies of the bones and muscles cannot be understood without a previous course in comparative anatomy; likewise other parts of the human body may be clarified, and what a difference in dissection if the student has already dissected a mammal!

Embryology is more important as a prerequisite to the study of anatomy than is comparative anatomy. The foldings of the brain; the separation of the hippocampus and the mammillary bodies from the frontal lobe; the development of the heart; the vestigial structures from the fetal circulation; the foldings of the peritoneum and of the alimentary canal, the fixation of the canal, its constrictions and dilatations, and the outgrowth of organs from it; the descent of the heart and diaphragm with the resultant position of the vagus and phrenic nerves; the non-descent of the testes; the relative length of the spinal cord and vertebral column resulting in the varying obliquity of the spinal nerves; the budding of the limbs and their growth as they drag along the muscles, nerves, and vessels to give them their ultimate course, relations, and distribution; to mention only a few of the multitudinous things that depend upon a knowledge of embryology will suffice to show that such knowledge is a prerequisite to the understanding of anatomy.

The great problem in teaching anatomy is how to combine the scientific and the practical in a subject of such vast detail and such multitudinous ramifications. There should be accuracy and thoroughness and at the same time the relation of anatomy should be taught as a foundation for anthropology, psychology, physiology, pathology, medicine, and surgery, each of which has equal value in a properly balanced medical course. It is inconceivable that in the time usually allotted to anatomy the student can make a careful dissection of all the structures of the body in their minutest details, learn these, and at the same time learn all the relations of anatomy to the six branches of the curriculum mentioned. The usual method is to do one thing or another, to teach anatomy as a science or to teach it as a trade, a tool for surgery. Some insist upon accuracy and thoroughness in dissection as the most important; others stress the relations to surgery and physical diagnosis; some teach 'physiological' anatomy; others 'philosophical' anatomy; some attempt digression into anthropology, some into pathology, others into psychology, still others make anatomy a basis for clinical medicine. Some advocate an entire revamping of the curriculum, and the

coordination in time of anatomy and other studies; whereas others would study by systems, so-called systematic anatomy, whereas still others would stress relations and topography. There is an element of truth, good sense, and right in almost all methods, yet no one can use all the good methods, nor can the good points of all methods be combined, but some good may be derived from many.

It seems necessary to insist on accuracy and thoroughness. The scientific side is important, therefore clean and careful dissecting is necessary, but the practical bearings of anatomy to subsequent study and practice cannot be overlooked. Probably the scientific and the practical are combined everywhere by different methods and with varying success.

The students and the traditions are different with the different schools, and that which gets results in one place might prove a failure in another. I have taught at places so absolutely different that the same methods throughout might have been disastrous. This may be illustrated by brief statements about each school where I have taught. The students at the Johns Hopkins must work independently. They are mature and have usually had courses in comparative anatomy and embryology. Their methods and habits vary, but the spirit of the place incites to drastic effort. Virginia students have the traditions of hard study and terrific examinations, through which have to be infused individual initiative and the perspective of research. The University of Michigan students have vigor and enterprise that need tone and direction; their traditions and environment lead naturally to research. The bigness of Tulane as the largest southern institution of medicine deepens responsibility and infuses ardor into the versatile students, but they need to become imbued with the value of research and the scientific spirit. The Filipino students have had twelve years or more of training in American schools, with two years in zoology, they come amply prepared, and, with their nimble wits and fingers, it is an easy matter to secure beautiful dissections, artistic reproductions by modeling, drawing, or painting, and to stir an interest in science. Unfortunately, flagging zeal or impaired health lead many aside.

It may not be amiss to give a few of the methods that have been used to apparent advantage.

The students, four to a subject, spend a short while on the thoracic and abdominal walls to familiarize themselves with the technique of dissecting and the recognition of structures. Then the abdomen and thorax are opened, the position of the organs is outlined in detail, the ramifications of the celomic cavities are explored, and the students make skeleton drawings of the basic parts of the alimentary and circulatory systems. This is supplemented later by the basic parts of the sympathetic and lymphatic systems, to which are finally added the peripheral parts as they are dissected. The body is turned over, and the basic parts of the bony, muscular and nervous systems are charted, to which may be added at least the peripheral nerves, thus securing charts of the great systems as a whole. Reconstruction of the principal pathways of the brain and cord as studied in cross-sections, and likewise of the organs from vertex to perineum are also required in their respective courses. Only by some such means as this does the student secure anything except a fragmentary or topographic idea of the body systems. The student learns the details and relations, and demonstrates them on the dissected part to the instructor.

It is especially desirable that the students reconstruct by chart the lymphatic system, because it is impossible to get any but a segmentary idea from dissecting the average cadaver, and the treatment is inadequate and incomplete in the text-books. The subject should be approached from two standpoints: the drainage of each organ or area, and the source of the lymph for any group of glands. Cancer of the liver secondary to cancer of the pancreas, pylorus, or mammary gland may be explained by the collateral circulation when certain groups of lymph glands are obstructed. The sources of infection for any group of glands should be known.

The charting of the spinal cord in situ, with the relation of the origin and exit of each nerve to the tips of the spinous processes and intervertebral discs, is illuminating to the student and the distribution in skin and muscle of the spinal as well as peripheral nerves is valuable in diagnosis.

Another method that has aroused enthusiasm among the students is the quiz-talk with demonstrations of prepared specimens, cross-sections, models, and charts. This method is especially valuable when a teacher has had considerable experience and the students have finished their dissection, and when given in connection with the course in topographic applied anatomy. An effort has been made to combine by adaptation the inimitable apt imagery of Osler with the illuminating magnetic method of Welch in drawing out students. A discussion of the number and value of valves in veins in relation to gravity and muscle action, the collateral circulation in lymphatics, bone growth, group muscle and nerve function, fascial sheaths, paralysis of nerves, anastomosis of arteries, blood and nerve supply of bone and joint, the mechanism of joints and of the pelvis in growth and sex, the lower extremity in stability and progression, the upper in delicate manipulation, to give but a few illustrations, serve to stimulate search beyond the text-book. Function is emphasized and the relations to medicine and surgery are stressed.

Beyond all else the broad fundamentals of anatomy are to be found in physical anthropology, the type and the race. Until the teaching of anatomy has its foundation in the types of man, it cannot be presented truly as it exists. There are many means of differentiating types, but the ear form is one of the most uniquely distinctive differentiators. I have been able to prove by the ear form alone differences of three meters in the length of the small intestine, of 500 grams in the weight of the liver of smaller amounts in the size of the brain, cerebellum, heart, kidneys and spleen; and difference in the shape and altitude of the organs in the abdomen; and in addition, if different human types represent different forms of intellect and differences in susceptibility and immunity to disease, then anthropology becomes the handmaiden of anatomy, an essential adjunct in its teaching.

Adult human types probably represent the end-products of chemical reactions that have been continuously at work throughout the life of the individual, or at least a large part of the life.

It is only fair to assume that the net result of this activity will be easier to perceive than the chemical reaction at any particular moment. It may be fruitless to attempt to determine or differentiate chemical types, but physical types have been established.

Anthropology has already established types of men, and at no distant date types of minds will also be established. These will play an ever-increasing part in medicine as their value is realized. Medicine has become one-sided through the study of the rôle of bacteria and kindred disease producers, to the neglect of the physical and psychical types and conditions. It is unnecessary to entail a discussion of the varying share of the incitor and host in the production of disease, or upon the immunity or susceptibility of the individual due to type or mental state, and it would be beside the mark. Once recognize the equal importance of the germ and of the man, the full value of the physical and psychical type and state, then follows as night the day the introduction of courses in anthropology and psychology on a par with pathology, physiology, or anatomy.

Dr. Goldthwaite, in the Shattuck lecture for 1915, presents the types of man as a basis for diagnosis and treatment, as do Percy Brown and Bryant. There is also an editorial in the number of the Journal which has the Shattuck lecture, wherein, with prophetic vision, the editor states that some medical school will give a course in anatomy based upon human types, others will follow until the custom becomes universal. Until anatomy is taught with the human types as a basis, it will not be taught as it exists. The structures of the body are found to vary about modes, each of which is normal and none of which is the average.

The writer has taught anatomy from the standpoint of types of men during the past ten years, both at Tulane and Virginia, during which time about 1,000 students have passed through this instruction. Other schools have in the meantime shown an interest in anthropology, as at Western Reserve and Washington University, and we may confidently look forward to the time when human types will be understood by the practitioner.

Such a piece of work as that published in *L'Anthropologie* by Dr. L. and Madame H. Hirschfeld may interest physiologists, pathologists, and internists. Serum tests were made during the Great War on about 500 soldiers in each of many national groups of Europe, of Asia, and of Africa, and differences that amounted to more than 50 per cent were found. The tests were so acute and positive that individual heredity could be determined, the parentage of any child verified.

Manouvrier and Godin have established types by skeletal form and through anthropometry on growing children, living adults, and the cadaver. Inspection aided by anthropometry will readily differentiate the types.

Chaillon divides the types into four: digestive, respiratory, muscular, and cerebral, from the physiological and clinical standpoint.

Mills has two types of visceral form, hypersthenic and asthenic, as determined through the x-ray by position, tonus, and motility. Bryant, following Treves and others, has the carnivorous and herbivorous types, as determined by the functions of the alimentary canal and by diet.

The phthisical and plethoric habitus are familiar to many physicians.

The temperaments, as depicted by Albrecht Dürer in the forms of four apostles and as taught at the school of Salerno, based upon the four elements and upon the four humors of Hippocrates and known as the melancholic, choleric, phlegmatic, and sanguine, are in disrepute among modern scientific physicians, but there is probably an element of truth in all. The evidence needs to be sifted, the physiological, psychological, and pathological characters of the physical types assorted and verified.

It still remains to be seen whether the hyperphylomorph, the macroskele, the cerebral, the asthenic, the narrow back, the habitus phthisicus, and the carnivorous are identical; likewise whether the mesophylomorph, the brachyskele, the digestive, the hypersthenic, the broad back, the plethoric, and the herbivorous are identical. The anthropologist is fast settling the basic

features of the physical type: it is high time for the psychologist, the physiologist, and the pathologist to get busy, to associate or dissociate the mental, functional, pathological, and physical types.

We cannot hope that anthropology and psychology will come into their own immediately as separate departments in the medical curriculum, which is already overcrowded, but short excursions into anthropology by the anatomist must suffice to impress upon the student the verity of the types and their relations to the practice of medicine. The students themselves serve as excellent models for the demonstration of the types.

We, in America, do not yet appreciate the scope of anthropology; only a few universities in this country provide for courses, but when we recognize its value then we may approach the variety and extent of the courses given at the *École d'Anthropologie de Paris* with its fifteen or more departments, each with its staff and laboratories.

The course in anthropology or psychology should have its place in the medical curriculum as a separate department with its corps of instructors, and the courses should be correlated with anatomy, physiology, pathology, and medicine.

Let us hope that the study of types of man will be pursued diligently in many directions, and that a place and time will be found in the medical curriculum, as the need and demand become imperative through the diffusion of knowledge.

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